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Taxonomic reappraisal of the *Hipposideros larvatus* species complex (Chiroptera: Hipposideridae) in the Greater and Lesser Sunda Islands, Indonesia

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Abstract

A total of 173 adult specimens of *Hipposideros* previously allocated to *H. larvatus* (*sensu lato*) was examined morphologically. Univariate and multivariate statistical analyses based on 31 skull and 16 external measurement were utilised and morphology of glans penis and baculum examined. These specimens came from islands in Nusa Tenggara (Sumbawa; Flores; Sumba; Savu; Roti; Semau and Timor) and a Western group (Madura; Java; Pulau Laut; Krakatau; Sumatra and Nias — with a few specimens from Peninsular Malaysia, Sarawak and Thailand).

Analysis of variance revealed that almost all skull and external characters differed significantly between locality groups; differences between locality groups greatly outweighed those due to adult age or sex effects.

The sharpest morphological boundary was between the Nusa Tenggara and Western Groups.

The Nusa Tenggara specimens represent *Hipposideros sumbae* Oei, 1960. Most Nusa Tenggara islands examined had populations with a distinctive morphology; those from Sumbawa and Roti were subspecifically distinct from the nominate subspecies on Sumba. The subspecific status of populations on Savu and Semau was indeterminate.

The Western group comprised three distinct taxa: *H. madurae* sp. nov. (two subspecies), *H. sorenseni* sp. nov. and *H. larvatus* (Horsfield, 1823). There was considerable variation in the latter species requiring considerably more study. A fourth taxon was recognised on West Java based on the distinctive shape of its baculum; its specific status will be determined following collection of additional specimens. Specimens from Peninsular Malaysia, and Sarawak were tentatively considered consubspecific with *H. l. larvatus* from W. Java, Sumatra, Pulau Laut, Krakatau and Nias. The single specimen from Thailand was smaller with a distinctive glans penis and baculum. It probably represents *Hipposideros grandis* G.M. Allen, 1936.

Introduction

Tate (1941) provided the first taxonomic appraisal of the forms of *Hipposideros larvatus* (Horsfield, 1823), a species he placed in the *H. speoris* group and diagnosed in some detail (Tate 1941: 377). Tate (op. cit.) stated that *H. larvatus* is easily distinguished from similar forms by the following combination of characters: anterior nasal horseshoe leaf with median cleft; forearm length 57 to 63 mm (but Tate 1941: 383 & 385 lists the forearm length of the *H. larvatus, H. deformis* and *H. vulgaris* holotypes as 53, 53 and 56 mm, respectively); tibia length 21-24 mm; ear emarginate; three lateral facial leaflets; transverse

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Figure 1 Map showing locality of specimens examined in this study.

noseleaf with three septa and four cells; and frontal sac present in both sexes. This diagnosis is further amplified slightly by Oey and van der Feen (1958) and Hill (1963).

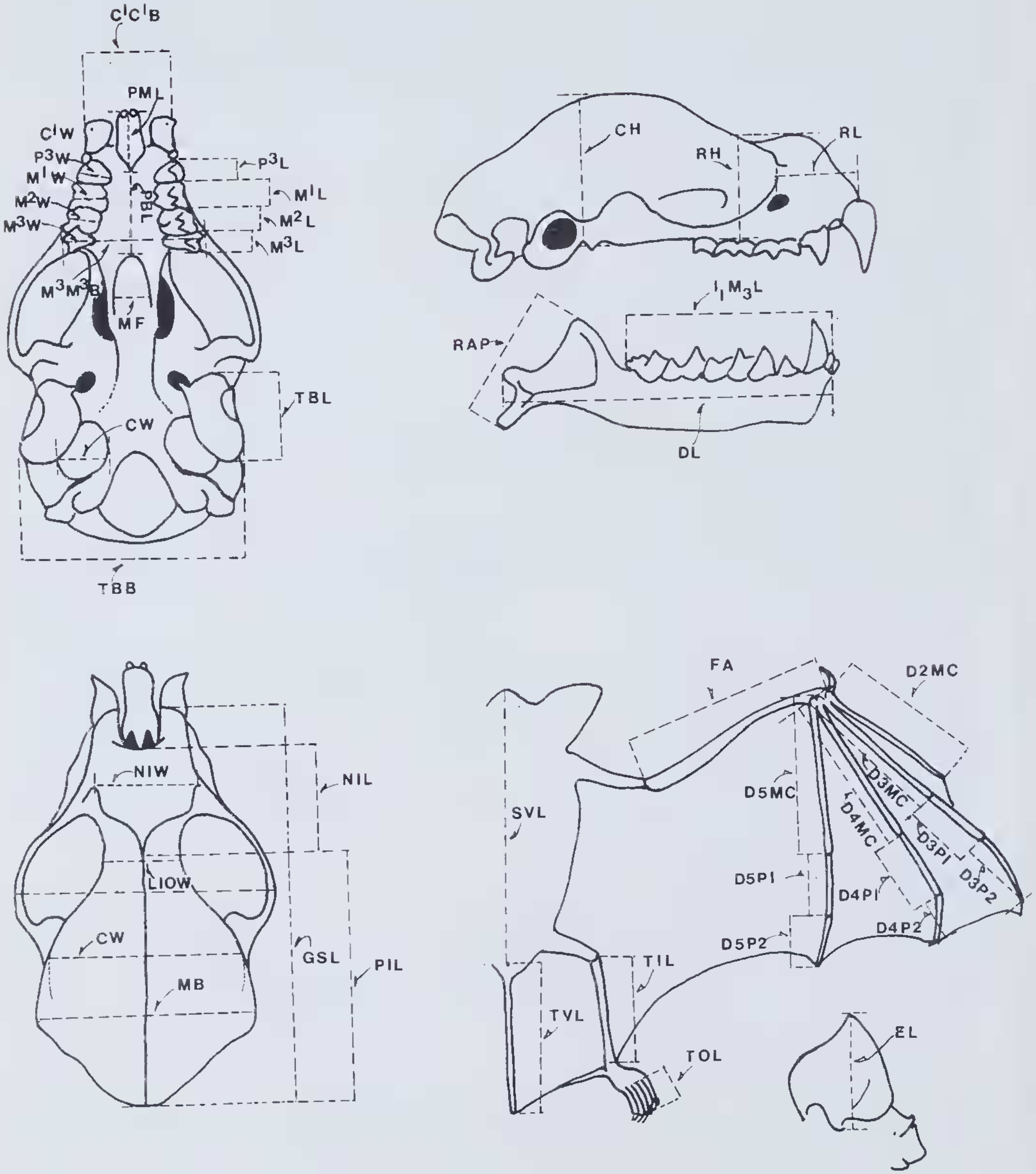
Tate (1941) lists the following subspecies or synonyms of *H. larvatus: H. insignis* (Horsfield, 1823) (Java); *H. deformis* (Horsfield, 1823) (Java); *H. vulgaris* (Horsfield, 1823) (Java); *H. leptophyllus* (Dobson, 1874) (Khasia Hills, Assam); *H. grandis* G.M. Allen, 1936 (Chindwin, Burma); *H. neglectus* Sody, 1936 (C. Borneo); *H. barbensis* Miller, 1900 (St Barbe I.) and *H. poutensis* J.A. Allen, 1906 (Hainan I., China). He studied a number of specimens of *H. larvatus* from Java, Borneo, Sumatra, Malay Peninsular, Thailand, Vietnam, Hainan and islands in the South China Sea. He concluded that throughout this range *H. larvatus* commonly showed a variation of from 3 to 4 mm in forearm length. He could not, however, detect differences in M^3 which was the basis of the original diagnosis of *H.l. grandis.* He also expressed doubts that *H. l. neglectus* was subspecifically distinct from the nominate subspecies. He thought it probable, though, that the Javanese forms *insignis, deformis* and *vulgaris* were probable synonyms of *H. larvatus.*

According to Oey and van der Feen (1958), Temminck (1835: 15) considered that Horsfield's form *vulgaris* was the female of *insignis* and that he could find no important differences between *insignis* and *H. larvatus.*

Hill (1963), in his classical revision of the genus *Hipposideros*, disagreed with Tate's (1941) comments in that he considered *neglectus* a valid subspecies and included in this subspecies specimens from Nias I. that Miller (1942: 116) thought may be separable from both *H. l. larvatus* and *H. l. neglectus.* He also agreed with Shamel (1942: 322) that *grandis* was subspecifically distinct from *neglectus.* Hill's (1963) classification of *H. larvatus* included the more recently described forms (*H. l. alongensis* Bourret, 1942 and *H. l. sumbae* Oei, 1960) and is as follows (distributions include additions by van Strien 1986):

H. l. larvatus (includes *vulgaris, deformis* and *insignis*) — Java, Kangean I.; Oey and van der Feen (1958) also list it on Bali I. but this is not confirmed.
H. l. leptophyllus — Khasi Hills, Assam.
H. l. barbensis — St Barbe I., S. China Sea.
H. l. poutensis — Pouten, Hainan I.
H. l. grandis — Akanti, upper Chindwin, Burma.
H. l. neglectus — Borneo; Karimata I., N. Pagai, Serasan I., S. Natuna I., Sumatra; Nias I., Simeulue I., Butang I., Malay Peninsular and Tioman I.
H. l. alongensis — Bay d'Along, Indochina.
H. l. sumbae — Sumba I. and Timor I.

Previous studies on the intraspecific taxonomy of *Hipposideros larvatus* have been superficial. Recognition of subspecies of *H. larvatus* has largely depended on a single character only, namely the length of the forearm (e.g., Sody 1936, Tate 1941) — although Oei (1960) and Shamel (1942) also briefly refer to larger or smaller cranial measurements when they diagnosed the forms *grandis* and *sumbae* and Hill (1963) provides cranial measurements for a number of subspecies of *H. larvatus.*


C¹C¹B
PML
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◀ **Figure 2** Measurement points of the skull and external characters of *Hipposideros* spp. recorded in this study. The description of the measurement codes are: GSL, greatest skull length; BW, braincase width; ZB, zygomatic breadth; MB, mastoid breadth; CH, cranial height-measured by placing lower arm of callipers against basisphenoid and basioccipital and upper arm to highest point on cranium, excluding sagittal crest; RH, rostrum height — from base of M^2 to highest point of nasal inflation; RL, rostrum length; LIOW, least interorbital width; PIL, cranial length; NIL, nasal inflation length; PBL, palatal bridge length; PML, premaxilla length; MF, mesopterygoid fossa width; TBL, tympanic bulla length; TBB, tympanic bulla breadth; NIW, nasal inflation width; CW, cochlea width; M^3M^3B, breadth across M^3 to M^3 from outer basal face; C^1C^1B, breadth across C^1C^1 from outer basal face; C^1W, P^3W, and $M^{1-3}W$ and P^3L, $M^{1-3}L$, maxillary teeth widths and lengths; I_1M_3L, lower tooth row length; DL, dentary length; RAP, distance from ramus to angular tip; SVL, snout to vent length; TVL, tail to vent length; EL, ear length; TIL, tibia length; TOL, toe (metatarsal and phalanges, exluding claw) length; FA, forearm length; D2MC, digit 2 metacarpal length; D3MC, digit 3 metacarpal length; D3P1, digit 3 phalanx 1 length; D3P2, digit 3 phalanx 2 length; D4MC, digit 4 metacarpal length; D4P1, digit 4 phalanx 1 length; D4P2, digit 4 phalanx 2 length; D5MC, digit 5 metacarpal length; D5P1, digit 5 phalanx 1 length; and D5P2, digit 5 phalanx 2 length.

We have available to us specimens previously allocated to *H. larvatus* (s. l.) from Java and Nusa Tenggara collected by us during the combined Western Australian Museum — Museum Zoologicum Bogoriense (MZB) expeditions of 1987-1991, as well as specimens in MZB that have not been previously reported upon. These are from islands in Nusa Tenggara (Sumbawa, Sumba, Roti, Savu, Semau, Timor) and Madura I., Pulau Laut I., Krakatau Is, Sumatra and Nias I., (as well as a few specimens from Peninsular Malaysia, Thailand and Borneo).

This paper presents the results and taxonomic conclusions of our examination of morphological variation of individuals within and between the above island populations.

Methods

A total of 173 adult specimens was examined in this morphometric comparison. The numbers of males and females from each locality (see Figure 1 for locality of specimens) is presented in Table 1. They are listed in the "Specimens Examined" section. All these specimens are currently lodged in the Western Australian Museum (WAM) or the Museum Zoologicum Bogoriense, Bogor (MZB). At the completion of this series of surveys half of all the WAM specimens, including the holotypes, will be lodged in MZB, Bogor.

Thirty one measurements of skull characters and 16 of external characters (all in mm), were recorded from adult specimens (see Figure 2, caption). In the graphical presentations in this paper, where a value represents more than one specimen the number of specimens is indicated.

Terminology used in the description of skull, dentary and dental (skull) characters and external characters follows Hill and Smith (1984). Pelage descriptions, when following the colour terminology of Smithe (1975), are capitalised.

Adults were diagnosed as those specimens with basioccipital and sphenoid bones completely fused and epiphyseal swellings absent from metacarpal joints. Additionally, three adult age classes were established based on extent of wear on the upper molar teeth: class 1, no wear or barely perceptible wear on M^{1-2} protocone; class 2, moderate wear on M^{1-2} protocone; class 3 heavy wear on M^{1-3} protocone (see Figure 3).

Sexual dimorphism of skull and external characters was investigated by multiple regressions on sex, age and locality group. Only specimens with a complete data set were included in these analyses. Consequently when the specimens from Semarang (Central Java) were included in the analysis the data set for external measurements was reduced to 13 characters. Snout to vent, tail to vent and ear lengths were excluded because these measurements were not recorded from the Semarang specimens and some of those from W. Java and Sumatra because they were 'cabinet' skins only.

Taxonomic considerations

In evaluating whether or not forms of *Hipposideros* examined in this study warranted recognition as distinct taxa, particular attention was given to the distinctness of skull, glans penis and baculum morphology. The latter was considered particularly important because Zubaid and Davison (1987) found that the morphology of the baculum was species-specific in all 10 species of *Hipposideros* they studied from Peninsular Malaysia. Pelage and overall body, wing and leg morphology were considered of secondary importance.

In this paper the canonical (discriminant) analyses (DFA) are presented after the systematic section. However, results of these analyses, particularly the relationships between specimens from different localities in discriminant function space, were important in recognising taxonomic groupings.

Systematics

Hipposideros larvatus larvatus (Horsfield, 1823)

Tables 1; Figures 1,4,5a,6a,7,8 and 9

Rhinolophus larvatus larvatus. Horsfield, T., 1823, Zoological Researches in Java and the neighbouring islands. No. 6.

Rhinolophus vulgaris Horsfield, T., 1823 Zool. Res. Java, No. 6, Java

Rhinolophus deformis Horsfield, T., 1823 Zool. Res. Java, No. 6, Java

Rhinolophus insignis Horsfield, T., 1823 Zool. Res. Java, No. 6, Java

Hipposideros larvatus neglectus Sody, 1936, Seventeen new generic, specific and subspecific names for Dutch East Indian mammals, Natuurk. Tijdschr. Ned-Ind. 96: 42-55, C. Borneo.

Holotype

British Museum (Natural History) number BM 79.11.21.93.

Type locality

Java.

Specimens examined

Listed in section "Specimens Examined".

Figure 3 Adult tooth wear categories. Class I, no wear or barely perceptible wear on M^1 protocone; class II, moderate wear on M^1 protocone; class III heavy wear on M^1 protocone.

Diagnosis

Hipposideros larvatus differs from *H. madurae* sp. nov. in averaging larger in most skull measurements. For example: greatest skull length 21.49 v. 20.84; zygomatic breadth 12.87 v. 12.23; C^1C^1 breadth 5.45 v. 5.11; mastoid breadth larger relative to both rostrum height (2.202 v. 2.120) and least interorbital width (with exception of two Pulau Laut specimens (Figure 7); C^1C^1 breadth averages larger relative to both nasal inflation length (0.945 v. 0.856) and I_1M_3 length (0.547 v. 0.523); cranial length longer relative to nasal inflation length (2.456 v. 2.263); tibia length averages larger (22.15 v. 19.32). Glans penis more laterally compressed distally with central distal fleshy lobe attached to baculum more elongate (Figure 6a). Baculum elongate and thin in dorsal profile, bifurcating distal arms long and thin rather than short and deep, basal area much smaller (Figure 5a).

It differs from *H. sorenseni* sp. nov., from which its skull is generally similar in size, in larger average C^1C^1 breadth (5.45 v. 5.34) and dentary angular to condyle length (5.87 v. 5.53). Glans penis distally more laterally compressed with distal fleshy lobe attached to baculum more elongate. Baculum less robust, in dorsal profile long and thin with broad basal pedestal, rather than basal half suboval, bifurcating distal arms much longer and thinner.

It differs from *Hipposideros sumbae* sp. nov. in averaging larger in most skull measurements (Table 1). For example: greatest skull length (21.49 v. 20.24); palatal bridge length (3.78 v. 3.41); nasal inflation length (5.77 v. 5.18); nasal inflation width (6.53 v. 6.24); and dentary length (15.20 v. 13.91); M^3M^3 breadth (8.70 v. 8.01); I_1M_3 length (9.96 v. 9.23). Palatal width relatively broader as indicated by M^3M^3 breadth relative to nasal inflation width (Figure 8); nasal inflation length larger relative to nasal inflation width (0.883 v. 0.830); cranial length shorter relative to nasal inflation length (2.456 v. 2.608); dentary length larger relative to rostrum length (Figure 9); Digit 5 phalanx 2 longer (10.88 v. 9.53-9.92); glans penis with distal end more laterally compressed and lateral profile square rather than gently rounded (Figure 6a). Baculum longer (1.07 v. 0.75-0.84) dorsal profile long and thin, with broad basal pedestal rather than basal half suboval, with long narrow rather than short broad bifurcated distal arms (Figure 5a).

Table 1 Measurements (in mm) for skull and external characters for male and female adults combined of *Hipposideros larvatus* (Indonesia); *H. madurae; H.m. madurae; H.m. jenningsi; H. sorenseni; H. larvatus* (Sarawak); *H. larvatus* (Malaya); *H.* sp. indet. (Sukabumi, W. Java); *H.* sp. *cf. grandis; H. sumbae* (total); *H. s. sumbae; H. s. rotiensis; H. s. sumbawae; H. sumbae* subsp. indet. A (Semau); *H. sumbae* subsp. indet. B (Savu) and *H. sumbae* cf. subsp. *rotiensis* (Timor). Explanation of measurement codes presented in Figure 2 caption.

CHARACTER TAXON		GSL	BW	ZB	MB	CH	RH	RL	LIOW	PIL	NIL	PBL
Hipposideros l.	N	60	60	60	60	60	60	60	60	60	60	60
larvatus	X	21.49	10.05	12.87	10.99	6.88	4.99	5.24	3.28	14.17	5.77	3.78
(W. Java, Pulau	SD	0.51	0.30	0.29	0.20	0.21	0.24	0.27	0.19	0.44	0.35	0.25
Laut, Krakatau,	MIN	20.38	9.33	11.83	10.42	6.46	4.51	4.76	2.90	13.01	5.02	3.32
Sumatra, Nias I)	MAX	22.76	10.66	13.48	11.32	7.34	5.68	5.95	3.66	15.13	6.58	4.34
Hipposideros madurae	N	15	15	15	15	15	15	15	15	15	15	15
(total)	X	20.84	9.50	12.23	10.52	6.61	4.97	5.27	3.17	13.51	5.97	3.71
	SD	0.36	0.21	0.26	0.23	0.16	0.37	0.20	0.16	0.24	0.28	0.15
	MIN	20.25	9.19	11.75	10.18	6.30	4.40	4.96	2.92	13.05	5.49	3.42
	MAX	21.62	9.91	12.78	10.91	6.89	5.43	5.59	3.44	13.92	6.45	3.98
Hipposideros madurae	N	8	8	8	8	8	8	8	8	8	8	8
madurae (Madura I.)	X	20.77	9.45	12.18	10.43	6.52	4.67	5.35	3.07	13.48	5.99	3.75
	SD	0.43	0.26	0.31	0.25	0.14	0.20	0.20	0.14	0.21	0.30	0.16
	MIN	20.25	9.19	11.75	10.18	6.30	4.40	5.09	2.92	13.29	5.49	3.48
	MAX	21.62	9.91	12.78	10.91	6.68	5.04	5.59	3.28	13.77	6.45	3.98
	N	7	7	7	7	7	7	7	7	7	7	7
Hipposideros madurae	X	20.92	9.56	12.29	10.63	6.72	5.32	5.18	3.27	13.55	5.94	3.67
jenningsi	SD	0.27	0.14	0.20	0.16	0.11	0.13	0.16	0.11	0.28	0.27	0.13
(Semarang-C. Java)	MIN	20.56	9.43	11.92	10.40	6.61	5.07	4.96	3.13	13.05	5.49	3.42
	MAX	21.39	9.79	12.50	10.88	6.89	5.43	5.47	3.44	13.92	6.21	3.82
Hipposideros	N	7	7	7	7	7	7	7	7	7	7	7
sorenseni	X	21.63	10.00	12.49	10.94	6.83	5.04	5.41	3.19	14.43	5.68	3.82
(Pangandaran-C/W	SD	0.33	0.13	0.17	0.19	0.23	0.27	0.21	0.10	0.43	0.40	0.14
Java)	MIN	21.15	9.83	12.34	10.58	6.62	4.75	5.06	3.00	13.65	4.83	3.56
	MAX	22.11	10.17	12.81	11.15	7.27	5.43	5.63	3.29	14.86	6.00	3.96
Hipposideros l. *larvatus* (Sarawak)	Value N = 1	22.04	9.90	13.67	11.20	6.85	4.85	5.32	3.70	14.27	6.32	3.99
Hipposideros l.	Value	22.36	10.58	13.32	11.29	7.07	5.04	5.45	3.53	13.79	6.45	3.86
larvatus (P. Malaysia)	N = 2	20.88	9.60	12.67	10.89	6.52	4.77	5.19	3.35	13.62	6.04	3.59
Hipposideros sp. indet	Value	21.08	9.88	12.10	10.80	6.60	4.98	5.37	3.14	13.82	5.56	3.74
(Sukabumi-W. Java)	N = 2	21.34	9.90	12.45	11.03	6.55	4.96	5.60	3.45	14.72	5.44	3.67
Hipposideros sp. cf. *H. grandis* (Thailand)	Value N = 1	21.07	9.74	12.14	10.67	6.74	4.63	5.48	3.47	13.45	6.30	3.68
Hipposideros sumbae	N	86	86	86	86	86	86	86	86	86	86	86
	X	20.24	9.44	11.89	10.29	6.52	4.79	5.17	3.14	13.51	5.18	3.41
	SD	0.45	0.26	0.32	0.20	0.16	0.24	0.24	0.18	0.30	0.27	0.18
	MIN	19.28	8.71	11.19	9.82	6.17	4.24	4.63	2.78	12.97	4.56	3.03
	MAX	21.26	10.01	12.79	10.76	6.91	5.49	5.78	3.64	14.69	5.88	3.93
Hipposideros sumbae	N	15	15	15	15	15	15	15	15	15	15	15
sumbae	X	20.57	9.68	12.12	10.49	6.51	4.75	5.39	3.08	13.46	5.30	3.45
	SD	0.30	0.20	0.20	0.15	0.12	0.24	0.17	0.09	0.23	0.28	0.21
	MIN	20.05	9.31	11.72	10.27	6.25	4.38	5.18	2.89	13.20	4.86	3.10
	MAX	20.99	10.01	12.48	10.76	6.73	5.33	5.60	3.20	13.88	5.87	3.93
Hipposideros sumbae	N	9	9	9	9	9	9	9	9	9	9	9
rotiensis	X	20.76	9.59	11.96	10.39	6.57	4.99	5.39	2.99	13.65	5.30	3.57
	SD	0.22	0.15	0.23	0.09	0.15	0.19	0.19	0.19	0.19	0.29	0.16
	MIN	20.55	9.35	11.80	10.26	6.33	4.70	5.17	2.78	13.38	4.88	3.36
	MAX	21.15	9.86	12.55	10.51	6.71	5.20	5.78	3.17	13.91	5.88	3.80
Hipposideros sumbae	N	54	54	54	54	54	54	54	54	54	54	54
sumbawae	X	20.01	9.34	11.80	10.20	6.51	4.76	5.04	3.20	13.48	5.11	3.36
	SD	0.35	0.21	0.29	0.18	0.16	0.23	0.19	0.18	0.32	0.25	0.16
	MIN	19.28	8.82	11.19	9.82	6.23	4.24	4.63	2.80	12.97	4.56	3.03
	MAX	20.84	9.89	12.38	10.60	6.91	5.29	5.48	3.64	14.69	5.63	3.83
Hipposideros sumbae	N	4	4	4	4	4	4	4	4	4	4	4
subsp. indet. A	X	20.78	9.72	12.15	10.42	6.72	4.71	5.25	2.96	13.86	5.36	3.37
(Semau)	SD	0.15	0.19	0.24	0.06	0.12	0.13	0.04	0.11	0.21	0.23	0.16
	MIN	20.60	9.52	11.80	10.36	6.60	4.58	5.20	2.80	13.65	5.12	3.13
	MAX	20.97	9.89	12.32	10.49	6.83	4.88	5.30	3.07	14.05	5.65	3.46
Hipposideros sumbae	N	3	3	3	3	3	3	3	3	3	3	3
subsp. indet. B	X	20.08	9.05	11.57	10.20	6.39	4.80	5.24	3.08	13.33	5.19	3.44
(Savu)	SD	0.08	0.30	0.30	0.12	0.21	0.14	0.12	0.07	0.20	0.10	0.18
	MIN	20.01	8.71	11.34	10.10	6.17	4.64	5.11	3.03	13.15	5.13	3.28
	MAX	20.17	9.30	11.91	10.33	6.59	4.90	5.32	3.16	13.55	5.30	3.63
Hipposideros sumbae	N	1	1	1	1	1	1	1	1	1	1	1
(Timor)	VALUE	21.26	9.70	12.79	10.62	6.50	5.49	5.46	2.87	14.18	5.42	3.56

PML	MF	TBL	TBB	NIW	CW	M^1M^1B	C^1C^1B	C^1W	P^1L	P^1W	M^1L	M^1W	M^2L
60	60	60	60	60	60	60	60	60	60	60	60	60	60
4.18	2.19	2.90	10.46	6.53	2.56	8.70	5.45	1.54	1.41	1.63	2.03	2.12	1.98
0.19	0.10	0.17	0.23	0.15	0.17	0.20	0.22	0.12	0.08	0.08	0.08	0.12	0.09
3.49	1.99	2.48	9.92	6.07	2.21	8.32	5.05	1.28	1.26	1.40	1.78	1.78	1.74
4.63	2.43	3.21	10.96	6.76	2.96	9.09	5.98	1.79	1.64	1.82	2.24	2.30	2.23
15	15	15	15	15	15	15	15	15	15	15	15	15	15
4.11	2.08	2.82	9.92	6.22	2.55	8.56	5.11	1.49	1.33	1.53	2.01	2.11	1.96
0.14	0.08	0.16	0.30	0.14	0.15	0.12	0.17	0.08	0.09	0.06	0.11	0.15	0.08
3.93	1.97	2.54	9.50	5.97	2.22	8.19	4.76	1.35	1.21	1.42	1.82	1.80	1.81
4.38	2.21	3.03	10.43	6.52	2.78	8.74	5.42	1.61	1.52	1.68	2.16	2.31	2.07
8	8	8	8	8	8	8	8	8	8	8	8	8	8
4.13	2.10	2.76	9.82	6.26	2.49	8.52	5.05	1.48	1.32	1.55	2.01	2.21	1.94
0.14	0.08	0.15	0.21	0.16	0.16	0.16	0.21	0.09	0.07	0.04	0.11	0.07	0.06
3.96	1.97	2.54	9.54	6.03	2.22	8.19	4.76	1.35	1.21	1.47	1.82	2.15	1.83
4.38	2.20	2.97	10.20	6.52	2.65	8.74	5.42	1.58	1.43	1.60	2.16	2.31	2.03
7	7	7	7	7	7	7	7	7	7	7	7	7	7
4.10	2.05	2.89	10.04	6.18	2.62	8.60	5.18	1.50	1.35	1.52	2.01	1.98	1.98
0.14	0.08	0.14	0.36	0.11	0.12	0.06	0.09	0.07	0.12	0.08	0.12	0.13	0.10
3.93	1.98	2.69	9.50	5.97	2.47	8.50	5.05	1.41	1.21	1.42	1.84	1.80	1.81
4.34	2.21	3.03	10.43	6.29	2.78	8.67	5.32	1.61	1.52	1.68	2.15	2.21	2.07
7	7	7	7	7	7	7	7	7	7	7	7	7	7
4.16	2.21	2.98	10.34	6.48	2.51	8.66	5.34	1.51	1.30	1.68	2.00	2.20	1.96
0.20	0.08	0.14	0.16	0.08	0.09	0.15	0.19	0.07	0.04	0.06	0.09	0.11	0.13
3.90	2.11	2.79	10.09	6.32	2.40	8.46	5.08	1.43	1.25	1.58	1.87	2.06	1.68
4.36	2.30	3.20	10.53	6.57	2.65	8.86	5.60	1.64	1.35	1.78	2.09	2.39	2.06
4.50	2.37	2.85	10.59	6.77	2.65	9.12	5.51	1.56	1.43	1.78	2.01	2.15	2.16
4.45	2.09	2.83	10.85	6.51	2.55	9.22	5.67	1.54	1.35	1.85	2.06	2.32	2.05
4.35	2.00	2.63	10.41	6.35	2.65	8.24	5.03	1.61	1.32	1.61	2.05	2.05	2.06
4.20	2.10	3.04	10.30	6.60	2.70	8.36	5.32	1.66	1.35	1.55	1.96	2.05	1.77
3.76	2.23	3.01	10.59	6.32	2.29	8.48	5.20	1.51	1.36	1.59	2.06	2.13	1.98
4.05	2.27	3.03	10.37	6.60	2.61	8.52	5.26	1.35	1.35	1.58	1.76	2.07	1.80
86	86	86	86	86	86	86	86	86	86	86	86	86	86
3.98	2.10	2.83	9.77	6.24	2.49	8.01	4.93	1.41	1.28	1.50	1.93	1.97	1.88
0.20	0.14	0.13	0.24	0.16	0.17	0.17	0.19	0.07	0.10	0.07	0.08	0.13	0.08
3.53	1.76	2.56	9.29	5.92	2.13	7.63	4.50	1.24	1.10	1.34	1.72	1.60	1.73
4.41	2.92	3.17	10.34	6.78	2.85	8.50	5.44	1.61	1.56	1.69	2.14	2.21	2.06
15	15	15	15	15	15	15	15	15	15	15	15	15	15
3.88	2.17	2.78	9.93	6.35	2.32	8.19	4.95	1.42	1.30	1.49	1.96	2.06	1.89
0.15	0.09	0.15	0.20	0.14	0.14	0.16	0.17	0.07	0.12	0.06	0.06	0.08	0.07
3.53	2.01	2.56	9.59	6.09	2.15	7.90	4.70	1.32	1.11	1.40	1.87	1.93	1.77
4.08	2.35	3.04	10.25	6.59	2.58	8.50	5.32	1.61	1.56	1.61	2.07	2.21	2.04
9	9	9	9	9	9	9	9	9	9	9	9	9	9
4.19	2.11	2.93	9.83	6.40	2.56	7.95	4.92	1.43	1.28	1.47	1.96	1.94	1.88
0.06	0.08	0.14	0.27	0.20	0.12	0.16	0.19	0.10	0.13	0.09	0.11	0.14	0.05
4.11	1.94	2.70	9.36	6.13	2.37	7.76	4.64	1.24	1.10	1.38	1.84	1.76	1.81
4.31	2.21	3.16	10.34	6.78	2.70	8.29	5.25	1.52	1.54	1.69	2.14	2.12	1.96
54	54	54	54	54	54	54	54	54	54	54	54	54	54
3.94	2.06	2.82	9.68	6.18	2.54	7.97	4.91	1.41	1.29	1.49	1.92	1.95	1.86
0.19	0.16	0.12	0.20	0.11	0.14	0.14	0.18	0.07	0.10	0.07	0.08	0.13	0.08
3.55	1.76	2.57	9.29	5.92	2.21	7.63	4.50	1.26	1.13	1.34	1.72	1.60	1.73
4.39	2.92	3.03	10.07	6.38	2.82	8.26	5.25	1.53	1.51	1.68	2.09	2.15	2.06
4	4	4	4	4	4	4	4	4	4	4	4	4	4
4.18	2.21	2.83	10.09	6.37	2.51	8.08	5.18	1.42	1.25	1.57	1.96	2.08	1.94
0.12	0.05	0.13	0.14	0.17	0.24	0.09	0.20	0.06	0.08	0.07	0.02	0.11	0.07
4.02	2.14	2.64	9.97	6.23	2.33	8.00	4.96	1.36	1.16	1.51	1.93	1.93	1.84
4.31	2.25	2.93	10.30	6.61	2.85	8.21	5.44	1.49	1.33	1.68	1.98	2.20	2.00
3	3	3	3	3	3	3	3	3	3	3	3	3	3
4.05	2.06	2.77	9.76	6.21	2.24	7.88	4.76	1.36	1.23	1.57	1.92	1.88	1.90
0.23	0.09	0.08	0.17	0.19	0.12	0.23	0.12	0.06	0.05	0.09	0.01	0.05	0.16
3.78	1.96	2.68	9.57	6.03	2.13	7.69	4.67	1.31	1.18	1.47	1.91	1.84	1.74
4.20	2.12	2.84	9.91	6.41	2.37	8.13	4.89	1.42	1.27	1.64	1.93	1.93	2.05
1	1	1	1	1	1	1	1	1	1	1	1	1	1
4.41	2.27	3.17	10.32	6.43	2.72	8.16	5.40	1.40	1.37	1.41	2.05	1.76	2.02

CHARACTER / TAXON		M^2W	M^1L	M^1W	I_1M_3L	DL	RAP	SVL	TVL
Hipposideros l. larvatus (W. Java, Pulau Laut, Krakatau, Sumatra, Nias I)	N	60	60	60	60	60	60	43	43
	X	2.35	1.28	1.89	9.96	15.20	5.87	55.68	30.46
	SD	0.14	0.05	0.08	0.23	0.32	0.25	2.50	2.42
	MIN	2.02	1.17	1.71	9.39	14.07	5.25	50.30	26.14
	MAX	2.58	1.45	2.07	10.44	16.07	6.66	61.23	35.43
Hipposideros madurae (total)	N	15	15	15	15	15	15	8	8
	X	2.30	1.28	1.92	9.78	14.65	5.65	56.11	27.69
	SD	0.18	0.05	0.07	0.30	0.29	0.29	2.14	2.74
	MIN	2.00	1.21	1.78	9.09	14.20	5.13	52.19	23.55
	MAX	2.56	1.40	2.05	10.21	15.15	6.09	58.90	30.91
Hipposideros madurae madurae (Madura I.)	N	8	8	8	8	8	8	8	8
	X	2.43	1.27	1.92	9.70	14.52	5.56	56.11	27.69
	SD	0.12	0.05	0.07	0.34	0.33	0.29	2.14	2.74
	MIN	2.24	1.21	1.78	9.09	14.20	5.13	52.19	23.55
	MAX	7.56	1.36	2.00	10.11	15.15	6.01	58.90	30.91
Hipposideros madurae jenningsi (Semarang-C. Java)	N	7	7	7	7	7	7	-	-
	X	2.16	1.30	1.92	9.88	14.80	5.74	-	-
	SD	0.11	0.06	0.08	0.22	0.17	0.27	-	-
	MIN	2.00	1.23	1.82	9.50	14.61	5.20	-	-
	MAX	2.31	1.40	2.05	10.21	15.02	6.09	-	-
Hipposideros sorenseni (Pangandaran-C/W Java)	N	7	7	7	7	7	7	6	6
	X	2.42	1.31	1.93	10.03	14.92	5.53	53.89	32.78
	SD	0.11	0.07	0.08	0.17	0.24	0.39	4.01	2.49
	MIN	2.18	1.22	1.82	9.77	14.42	5.00	50.16	30.07
	MAX	2.50	1.39	2.02	10.23	15.16	6.10	60.00	36.20
Hipposideros l. larvatus (Sarawak)	Value N = 1	2.38	1.37	1.96	10.79	15.45	6.33	56.73	29.93
Hipposideros l. larvatus (P. Malaysia)	Value N = 2	2.51	1.33	1.84	10.63	15.64	5.90	60.09	33.10
		2.31	1.31	1.93	10.01	15.21	5.97	57.99	34.62
Hipposideros sp. indet. (Sukabumi-W. Java)	Value N = 2	2.37	1.25	1.84	10.00	14.88	5.73	51.78	28.79
		2.19	1.24	1.86	9.89	14.96	5.80	56.73	30.79
Hipposideros sp. cf. *H. grandis* (Thailand)	Value N = 1	2.39	1.30	1.84	9.52	14.27	5.61	57.23	31.77
Hipposideros sumbae	N	86	86	86	86	86	86	72	71
	X	2.19	1.22	1.78	9.23	13.91	5.50	52.34	28.26
	SD	0.11	0.05	0.09	0.24	0.37	0.30	2.20	2.03
	MIN	1.84	1.10	1.52	8.48	13.09	4.60	47.67	24.05
	MAX	2.48	1.32	1.95	9.76	14.81	6.08	58.97	32.55
Hipposideros sumbae sumbae	N	15	15	15	15	15	15	15	15
	X	2.26	1.24	1.84	9.40	14.17	5.49	52.43	28.73
	SD	0.07	0.05	0.05	0.20	0.34	0.28	1.71	2.16
	MIN	2.11	1.16	1.75	9.08	13.54	4.82	49.80	24.78
	MAX	2.40	1.32	1.95	9.76	14.81	5.92	56.04	32.55
Hipposideros sumbae rotiensis	N	9	9	9	9	9	9	9	8
	X	2.17	1.20	1.73	9.27	14.10	5.63	51.60	30.23
	SD	0.05	0.06	0.05	0.23	0.21	0.43	2.72	1.44
	MIN	2.09	1.10	1.66	9.00	13.77	4.86	47.80	27.53
	MAX	2.24	1.28	1.83	9.69	14.43	5.96	55.20	32.14
Hipposideros sumbae sumbawae	N	54	54	54	54	54	54	41	41
	X	2.17	1.22	1.78	9.16	13.77	5.45	52.68	27.88
	SD	0.12	0.04	0.09	0.22	0.34	0.26	2.14	1.93
	MIN	1.84	1.12	1.52	8.48	13.09	4.60	48.65	24.05
	MAX	2.48	1.32	1.94	9.58	14.28	5.96	58.97	31.60
Hipposideros sumbae subsp. indet. A (Semau)	N	4	4	4	4	4	4	4	4
	X	2.28	1.22	1.81	9.36	14.24	5.81	49.52	27.65
	SD	0.14	0.06	0.08	0.09	0.15	0.32	2.22	1.70
	MIN	2.10	1.15	1.72	9.25	14.09	5.41	47.67	26.16
	MAX	2.40	1.28	1.87	9.44	14.40	6.08	52.27	30.09
Hipposideros sumbae subsp. indet. B (Savu)	N	3	3	3	3	3	3	3	3
	X	2.20	1.18	1.69	9.19	13.79	5.43	53.17	26.56
	SD	0.04	0.02	0.08	0.42	0.19	0.33	0.60	0.63
	MIN	2.15	1.16	1.61	8.72	13.64	5.11	52.79	25.86
	MAX	2.23	1.20	1.77	9.52	14.00	5.77	53.87	27.08
Hipposideros sumbae (Timor)	N	1	1	1	1	1	1		
	VALUE	2.00	1.26	1.76	9.25	14.73	6.08		

EL	TIL	TOL	FA	D2MC	D3MC	D3P1	D3P2	D4MC	D4P1	D4P2	D5MC	D5P1	D5P2
43	59	60	60	60	60	60	60	60	60	60	60	60	60
20.94	22.15	5.05	57.47	45.70	42.89	19.13	19.61	42.01	13.54	10.11	38.03	14.79	10.88
1.14	1.42	0.41	2.00	1.75	1.59	0.87	1.29	1.49	0.68	0.61	1.32	0.69	0.65
18.56	18.37	3.99	53.19	42.48	39.20	16.44	16.84	39.04	12.22	8.68	35.28	12.77	9.82
23.31	24.83	5.78	62.05	49.84	46.15	20.90	22.39	45.33	15.64	12.07	41.21	16.37	15.52
8	15	15	15	15	15	15	15	15	15	15	15	15	15
20.13	19.32	4.55	54.96	43.79	41.27	18.81	18.12	39.89	13.24	9.85	36.00	14.37	10.44
0.57	1.03	0.40	1.39	1.48	1.20	0.94	1.17	1.20	0.93	0.68	1.25	0.68	0.42
19.61	17.58	3.96	53.13	40.56	38.85	17.41	14.84	37.60	12.01	8.71	33.60	12.90	9.98
21.23	20.81	5.14	57.93	46.35	43.28	20.45	19.88	42.28	15.74	11.04	38.69	15.87	11.33
8	8	8	8	8	8	8	8	8	8	8	8	8	8
20.13	19.66	4.85	54.91	43.43	40.88	18.52	18.41	39.41	12.66	9.48	35.77	14.06	10.44
0.57	0.77	0.22	1.03	1.66	1.32	0.75	0.71	1.21	0.44	0.63	1.30	0.49	0.38
19.61	18.34	4.58	53.58	40.56	38.85	17.41	17.39	37.60	12.01	8.71	33.60	12.90	10.04
21.23	20.59	5.14	56.09	45.71	42.05	19.83	19.88	40.99	13.44	10.51	37.20	14.46	11.05
-	7	7	7	7	7	7	7	7	7	7	7	7	7
-	18.94	4.19	55.01	44.20	41.72	19.13	17.79	40.45	13.91	10.28	36.27	14.74	10.45
-	1.21	0.23	1.81	1.24	0.93	1.08	1.50	0.99	0.90	0.46	1.23	0.71	0.50
-	17.58	3.96	53.13	42.64	40.52	17.72	14.84	39.25	12.87	9.64	34.95	13.77	9.98
-	20.81	4.66	57.93	46.35	43.28	20.45	19.44	42.28	15.74	11.04	38.69	15.87	11.33
6	7	7	7	7	7	7	7	7	7	7	7	7	7
21.20	21.97	4.59	57.52	46.23	43.41	18.99	19.80	41.69	13.67	10.08	35.51	14.83	10.91
1.09	0.75	0.33	1.55	0.86	0.43	0.42	0.76	1.37	0.61	0.83	1.49	0.44	0.70
20.16	21.38	4.19	55.41	44.79	42.58	18.45	18.78	39.18	12.96	9.13	35.81	14.14	10.05
22.78	23.31	5.11	60.22	47.65	43.95	19.68	20.70	43.19	14.83	11.37	39.84	15.45	12.06
20.21	21.98	5.40	56.89	47.03	44.00	18.58	19.02	41.61	13.35	10.74	38.50	14.75	10.64
20.46	22.65	5.08	57.82	46.82	43.80	19.94	20.34	42.32	14.25	11.06	38.26	15.36	12.17
20.18	22.49	5.18	59.24	47.24	44.53	18.70	20.04	43.11	13.18	10.63	39.08	15.47	10.79
22.46	22.17	5.04	56.47	45.20	42.71	18.59	19.09	42.22	13.27	10.31	37.34	13.96	10.50
22.38	22.51	4.99	58.65	45.03	42.70	20.13	20.36	42.26	12.79	10.45	38.49	14.26	11.05
23.23	21.48	5.22	54.01	43.58	40.76	17.30	18.10	40.51	13.89	9.62	36.55	14.86	9.82
72	86	86	86	86	86	86	86	86	86	86	86	86	86
21.14	19.59	4.96	54.00	42.97	40.48	17.62	17.95	39.01	39.01	12.98	8.99	35.44	9.74
1.06	0.75	0.37	1.44	1.25	1.05	0.72	1.01	0.97	0.97	0.53	0.53	0.84	0.53
19.11	17.38	3.90	49.86	39.57	38.17	15.20	14.97	36.39	36.39	11.62	7.39	33.34	8.46
23.77	21.24	5.59	57.02	45.59	43.44	19.07	20.54	40.98	40.98	14.73	10.05	37.30	11.11
15	15	15	15	15	15	15	15	15	15	15	15	15	15
21.81	19.83	5.15	54.34	43.26	40.78	17.53	17.77	39.39	39.39	12.99	8.82	35.62	9.55
0.91	0.67	0.12	0.96	1.25	1.02	0.52	0.51	0.80	0.80	0.43	0.36	0.75	0.32
20.37	19.03	4.94	52.34	40.68	38.82	16.69	17.17	37.79	37.79	12.15	8.29	34.43	9.03
23.04	21.24	5.37	55.55	45.07	43.08	18.64	19.08	40.46	40.46	13.57	9.54	37.30	9.99
9	9	9	9	9	9	9	9	9	9	9	9	9	9
22.46	20.23	5.21	53.83	43.31	40.50	18.36	18.84	39.44	39.44	13.50	8.99	35.78	9.92
0.86	0.49	0.16	1.61	0.74	0.43	0.37	0.71	0.36	0.36	0.30	0.17	0.42	0.44
21.12	19.29	5.02	51.89	42.21	40.01	17.98	17.89	38.80	38.80	13.06	8.78	35.11	9.43
23.77	21.03	5.43	55.84	44.48	41.46	18.98	20.15	39.85	39.85	14.00	9.28	36.40	10.61
41	54	54	54	54	54	54	54	54	54	54	54	54	54
20.51	19.41	4.85	53.92	42.90	40.44	17.43	17.85	38.87	12.87	9.03	35.35	14.28	9.76
0.61	0.77	0.42	1.52	1.29	1.09	0.71	1.10	0.98	0.53	0.61	0.86	0.56	0.54
19.11	17.38	3.90	49.86	39.57	38.17	15.20	14.97	36.39	11.62	7.39	33.34	12.45	8.59
21.61	20.88	5.59	57.05	45.59	43.44	18.96	20.54	40.97	14.73	10.05	37.14	15.31	11.11
4	4	4	4	4	4	4	4	4	4	4	4	4	4
22.06	19.76	5.08	54.17	42.36	40.32	18.47	17.93	39.27	13.26	8.96	35.61	14.08	9.53
1.13	0.79	0.22	1.99	1.79	1.28	0.53	0.66	1.59	0.82	0.67	1.18	0.85	0.82
20.84	18.84	4.81	52.03	40.11	38.69	17.80	17.03	37.31	12.23	8.35	34.14	13.09	8.46
23.29	20.58	5.30	56.13	44.31	41.68	19.07	18.57	40.98	14.05	9.76	36.84	14.85	10.41
3	3	3	3	3	3	3	3	3	3	3	3	3	3
21.14	19.69	5.02	54.12	42.09	39.48	17.84	17.71	37.67	12.84	9.01	34.66	13.97	9.65
0.89	0.27	0.12	1.50	0.73	1.26	0.56	1.48	0.44	0.23	0.42	1.12	0.67	0.39
20.11	19.52	4.89	52.79	41.59	38.23	17.20	16.00	37.23	12.58	8.54	33.81	13.23	9.22
21.75	20.00	5.12	55.79	42.93	40.74	18.23	18.60	38.11	13.03	9.35	35.93	14.53	9.99

Description

Skull (Table 1, Figures 4, 7-9)

Cranium long relative to nasal length (2.456), lateral profile gently sloping to posteriormost point but a little more sharply sloping approaching junction of sagittal and lambdoidal crests; premaxilla-maxilla ventral junction U or V shaped; sagittal crest well developed but posterior one-quarter weak and barely reaching lambdoidal crest; supraorbital ridges moderately well developed and diverge sharply from junction with sagittal crest; nasal inflation with curved posterolateral edges; nasal inflation moderate; frontal depression shallow; rostral eminences moderately inflated, separated by shallow groove; nasal inflation lateral profile subrounded to only slightly arched; anteorbital foramen elongate and separated from orbit by moderately wide bar; maxilla generally encloses slightly elongate palatal foramen but occasionally do not enclose this foramen or do so only partially; posterior palatal margin usually U shaped, occasionally slightly more sharply angled; vomer projects posterior of palatal shelf; sphenoid bridge parallel sided or very slightly expanded posteriorly, from ventral aspect almost conceals sphenorbital sinus above, moderately deep median groove; C^1 with low anterior cusp, posterior cusp absent; PM^2 slightly extruded from toothrow, compressed tightly between C^1 and PM^4 (which are in contact or nearly so); PM_2 moderately large usually three-quarters length of PM_4.

Externals

Anterior noseleaf with small but distinct median emargination; occasionally this emargination supported by small tongue like protrusion beyond margin of leaf; three accessory lateral leaflets; internarial septum only very slightly inflated but its width not exceeding *c.* 0.7 mm; narial lappets well developed height above surface of anterior noseleaf *c.* 0.6 mm; nostril slightly pocketed; intermediate leaf width only slightly less than that of anterior noseleaf, with moderate median swelling and weaker lateral swellings; posterior leaf moderate with three well defined septa, upper edge semicircular; frontal sac in both sexes, but in females reduced to a depression, often shallow with a tuft of hair; ear with small process at antitragal fold.

Pelage

Dorsal surface with basal two-thirds of hairs Cream Color to Straw Yellow tipped with Fawn Color to Russet. This tipping dominates colour of back and forehead but is only very light on shoulders, neck and face such that under colour emerges as a pale cape of hair in these parts. Throat and chin hairs Cinnamon to Straw Yellow, while venter a darker Drab to Smoke Gray. Wing membranes and ears Burnt Umber.

Glans penis (Figure 6a)

The glans penis was examined from specimens from Ciampea, Ujong Kulon, Carita (W. Java), Krakatau Is, Aceh (N. Sumatra) and Nias I. The glans distal part laterally compressed such that the distal lobe covering cranial arms of baculum elongate. In lateral profile, distal end of glans slightly flared with the anterodorsal part projected slightly more so than the corresponding ventral part dorsal slit about 1.2 mm long, such that when lateral distal flanges widened it exposed large urethral vestible.

Figure 4 Photograph of skull and dentary of *Hipposideros l. larvatus,* MZB 1415, Krakatau Is; ventral view as stereopair. Scale line 5 mm.

Baculum (Figure 5a)

Short, base 0.51 ± 0.048 (N = 8) wide, total length 1.07 ± 0.068(8). Almost three quarters of length baculum comprises bifurcating arms from base, distal one quarter of arms inflected sharply cranially to a height above the base of 0.51 ± 0.078(8).

Distribution

W. Java, Palau Laut, Krakatau Is, Sumatra, Nias I., probably Peninsular Malaysia and Borneo (Figure 1).

Referred specimens

Two specimens from Pahang, Peninsular Malaysia and one from Sarawak were examined and measured. They had a glans penis and baculum that were very similar to *H. l. larvatus*. Further, when these three specimens were included in the DFA they clustered with the *H. l. larvatus* group.

Hipposideros madurae sp. nov.

Table 1; Figures 1,5b,c,6b,7-9,17,20-21

Diagnosis

Hipposideros madurae differs from *Hipposideros larvatus* in having a generally smaller skull (Table 1). For example greatest skull length (20.84 v. 21.49); zygomatic breadth (12.23 v. 12.87); C^1C^1 breadth (5.11 v. 5.45); mastoid breadth shorter relative to rostrum height (2.120 v. 2.202) and least interorbital width (with exception of two Pulau Laut specimens (Figure 7); C^1C^1 breadth averages shorter relative to nasal inflation length (0.856 v. 0.945) and I_1-M_3 length (0.523 v. 0.547); cranial length shorter relative to nasal inflation length (2.263 v. 2.456). Tibia length averages smaller (19.32 v. 22.15). Glans penis less laterally compressed distally with central distal fleshy lobe attached to baculum more elongate (Figure 6a & b). Baculum oval in dorsal outline rather than elongate, bifurcating distal arms short and deep rather than long and thin, basal area much larger (Figures 5a,b,c,6a,b).

It differs from *Hipposideros sorenseni* in having a generally smaller skull (Table 1). For example: greatest skull length (20.84 v. 21.63); braincase width (9.50 v. 10.00); zygomatic breadth (12.23 v. 12.49); cranial length (13.51 v. 14.43); greatest skull length averages shorter relative to nasal inflation length (3.491 v. 3.808); mastoid breadth narrower relative to least interorbital width (Figure 7); cranial length shorter relative to nasal inflation length (2.263 v. 2.541). Digit 5 metacarpal length smaller relative to toe length (Figure 17); tibia length smaller relative to toe length (Figure 18). Baculum shorter (0.75-0.93 v. 1.15-1.20), distal bifurcating arms relatively longer with concomitant shorter solid basal part (Figure 5b,c and d).

It differs from *H. sumbae* by averaging larger in most skull measurements (see Table 1). For example, greatest skull length (20.84 v. 20.24); palatal bridge length (3.71 v. 3.41); nasal inflation length (5.97 v. 5.18); dentary length (14.65 v. 13.91); M^3-M^3 breadth (8.56 v. 8.01); I_1-M_3 length (9.78 v. 9.23). Palatal width relatively broader as indicated by outside M^3M^3 breadth relative to nasal inflation width (Figure 8). Nasal inflation length relative to nasal inflation width averages much larger (0.960 v. 0.830); cranial length relatively shorter relative to nasal inflation length (2.263 v. 2.608); dentary length larger relative to rostrum length (Figure 9). Digit 5 phalanx 2 longer (10.45-10.91 v. 9.53-9.92). Glans penis with distal outline squarer in lateral profile, central distal lobe more vertical (Figure 6b and c). Baculum more robust, distal bifurcating arms longer with concomitant shorter base, cranial projection of arms taller with distal edge more vertical (Figure 5b,c and e).

Hipposideros madurae madurae subsp. nov.

Table 1; Figures 1,5b,6b,10,18,20

Holotype

Museum Zoologicum Bogoriense, MZB 10613B, adult male, carcase in alcohol, penis intact, skull separate.

Type locality

Sampang, Pulau Madura (Madura I.) nr NE Java (7° 13′S; 113° 15′E); altitude 0-30 m..

Paratypes

Listed in section "Specimens Examined".

Diagnosis

Hipposideros m. madurae differs from *H. m. jenningsi* sp. nov. in having a generally slightly smaller skull (Table 1). Rostrum height shorter relative to both nasal inflation length (0.780 v. 0.896) and mastoid breadth (Figure 10); cranial height smaller relative to nasal inflation length (1.089 v. 1.131); least interorbital width smaller relative to nasal inflation length (0.513 v. 0.551); toe length longer relative to tibia length (Figure 18).

Description

Skull (Table 1; Figure 20)

Skull as for *H. l. larvatus* but skull smaller; zygomatic breadth narrower; C^1C^1 breadth narrower; supraorbital ridges tend to be weaker and diverge less sharply from junction with sagittal crest; frontal depression very shallow; rostrum tends to be flatter; mesopterygoid fossa tends to be narrower with palation squarer and occasionally (MZB 10613F and MZB 10615B) with a tiny postpalatal projection; sphenoidal bridge parallel sided and conceals considerably less of sphenorbital sinus.

Externals (Table 1)

As for *H. l. larvatus.*

Glans Penis (Figure 6b)

Distal view suboval with central fleshy lobe attached to baculum subrectangular; this distal lobe with moderately large basal oval eminences projecting anterior of lobe; distal tip in lateral view only very slightly flared with anterior margin almost vertical; dorsal slit *c.* 1.1 mm long, such that when lateral distal flanges widened urethral vestible large.

Baculum (Figure 5b)

Baculum short (greatest length 0.75-0.82, N = 2); with wide (0.59 - 0.60) robust basal part; bifurcating distal arms short, a little more than half basal length, with cranial projecting part robust and 0.75-0.82 above basal part. Anterior edge of cranial arms almost vertical.

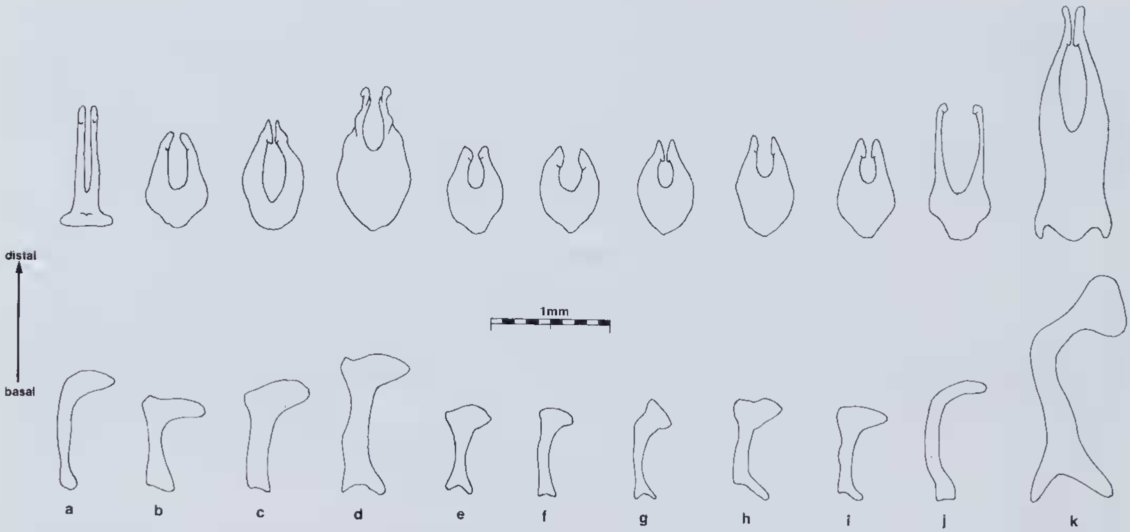


Figure 5 Baculum of forms of *Hipposideros* studied (top, dorsal view; bottom, lateral view). (a) *H. l. larvatus* (WAM M23305); (b) *H. m. madurae* (MZB 10613c); (c) *H. m. jenningsi* (MZB 14855); (d) *H. sorenseni* (MZB 10612A); (e) *H. s. sumbae* (WAM M30338); (f) *H. s. rotiensis* (WAM M35369); (g) *H. s. sumbawae* (WAM M31553); (h) *H. sumbae* subsp. indet. A (WAM M38017) (Semau I.); (i) *H. sumbae* subsp. indet. B (WAM M35259) (Savu I.); (j) *H.* sp. indet. (WAM M30009) (Sukabumi, W. Java); and (k) *Hipposideros* sp. cf. *H. grandis* (WAM M26828) (Thailand).

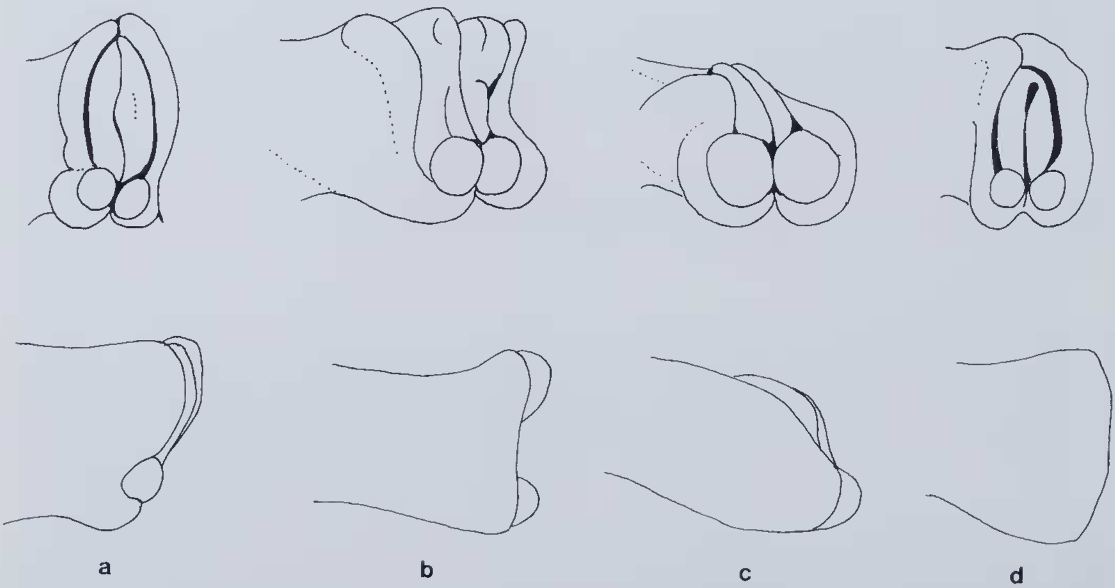


Figure 6 Glans penis of (a) *Hipposideros l. larvatus*; (b) *H. madurae*; (c) *H. sumbae*; and (d) *H.* sp. cf. *H. grandis* (Thailand). (Top row, oblique view; bottom row, lateral view).

Distribution

Madura I., Indonesia.

Etymology

Named after Madura I.

Hipposideros madurae jenningsi subsp. nov.

Table 1; Figures 1,5c,6b,10,18 and 21

Holotype

Museum Zoologicum Bogoriense, MZB14883 (collection number 103/40), adult female, 'puppet skin', skull separate, collected 29 February 1940 by A. V. Von Bemmel.

Type locality

Goa (≡ cave) Landak, near Desa (village), Karang Sagung, Semarang district, C. Java (*c.* 6°58'S, 110°29'E).

Paratypes

Listed in section "Specimens Examined".

Diagnosis

Hipposideros m. jenningsi differs from *H. m. madurae* in the characters indicated above in the diagnosis of that subspecies.

Description

Skull (Table 1, Figure 21)

As for *H. l. larvatus* but skull smaller, particularly nasal length relative to cranial length; zygomatic breadth narrower; C^1C^1 breadth narrower; supraorbital ridges tend to be weaker; frontal depression very shallow; rostrum tends to be flatter; mesopterygoid fossa tends to be a sharper U shape, occasionally (MZB 14862) with a tiny postpalatal projection; sphenoidal bridge parallel sided and conceals considerably less of sphenorbital sinus.

Externals (Table 1)

As for *H. l. larvatus.*

Glans penis

Similar to *H. m. madurae* (see Figure 6b).

Baculum (Figure 5c)

Similar to *H. m. madurae* but a little larger (0.93 v. 0.75-0.82) and with distal bifurcating arms a little longer relative to basal part.

Distribution

Near Semarang, C. Java, Indonesia (Figure 1).

Etymology

Named after Dr Gerald B. Jennings, Head Division of Virology, U.S. Naval Medical Research Unit No. 2, Jakarta Detachment, in recognition of his many kindnesses in assisting staff of the Western Australian Museum/Museum Zoologicum Bogoriense with their research programme in Indonesia.

Figures 7-19 Univariate plots of skull and external characters of *H. larvatus* (▽); *H. m. madurae* (O); *H. m. jenningsi* (□); *H. sorenseni* (△); *H.* sp. indet. (Sukabumi) (◇); *H. s. sumbae* (•); *H. s. rotiensis* (■); *H. s. sumbawae* (▲); *H. sumbae* subsp. indet A (Semau) (▼); *H. sumbae* subsp. indet. B (Savu) (◆) and Timor (ø).

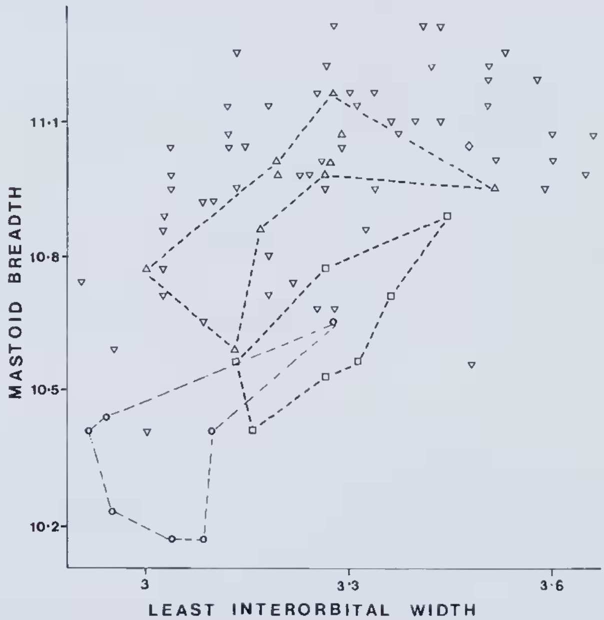


Figure 7 Mastoid breadth *versus* least interorbital width.

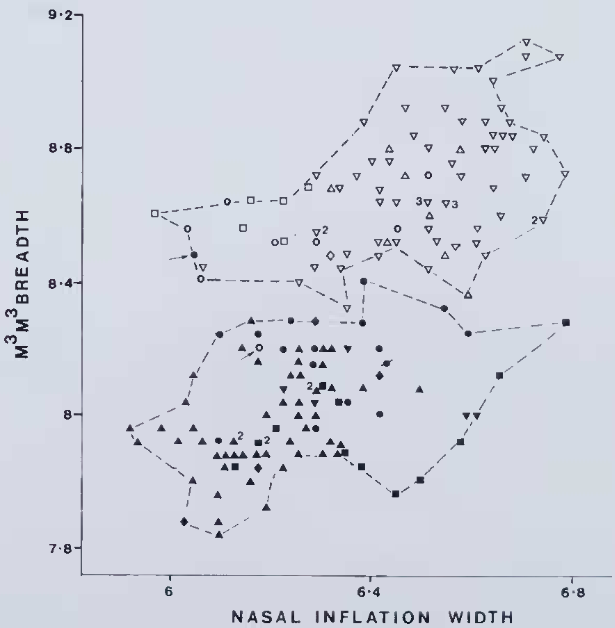


Figure 8 M^3M^3 breadth *versus* nasal inflation width.

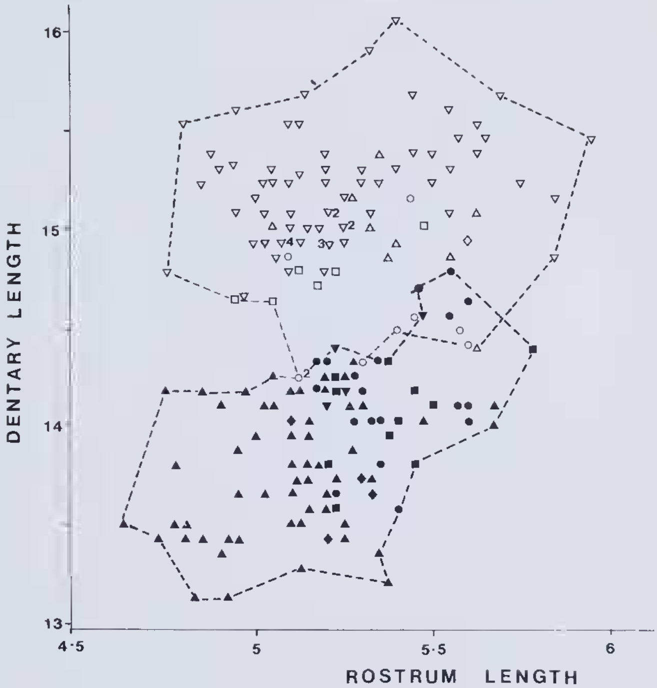


Figure 9 Dentary length *versus* rostrum length.

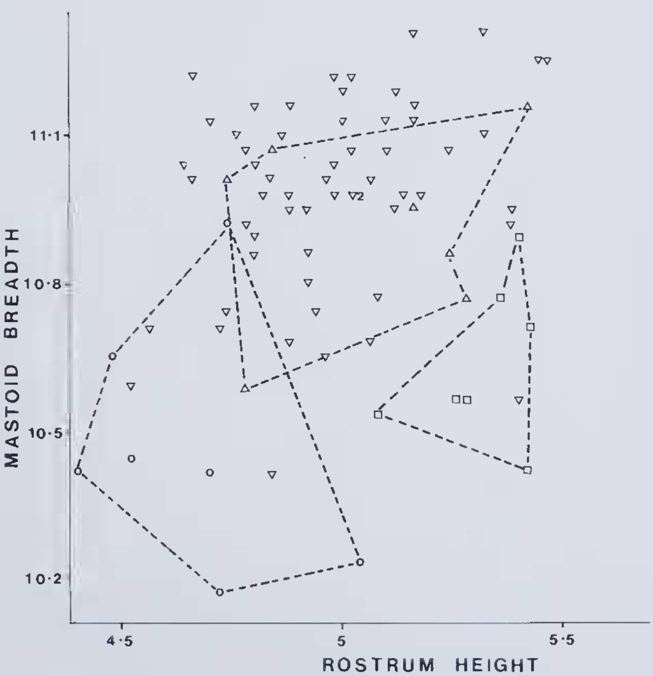


Figure 10 Rostrum height *versus* mastoid breadth.

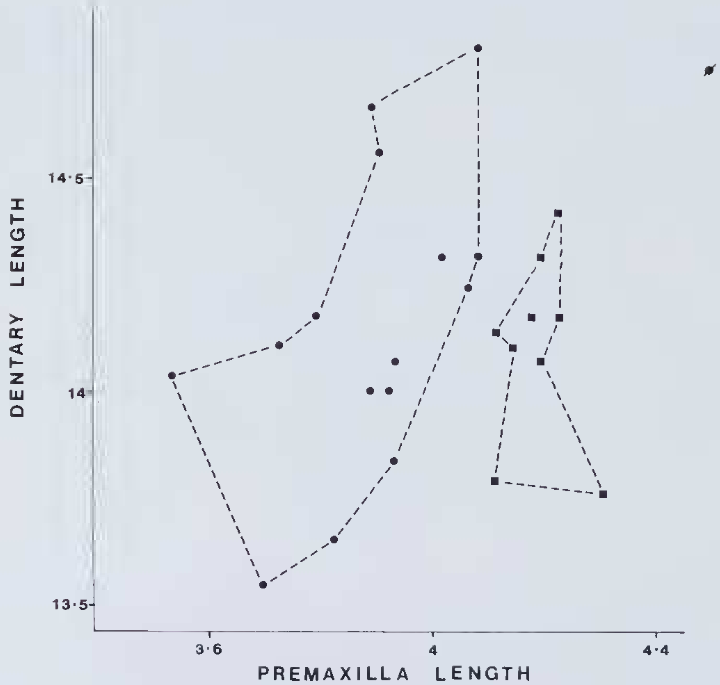


Figure 11 Dentary length *versus* mesopterygoid fossa width.

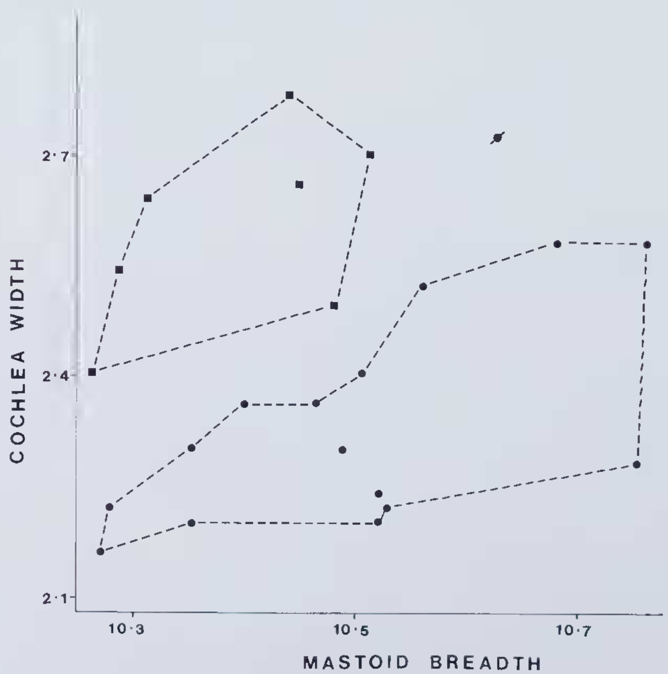


Figure 12 Cochlea width *versus* mastoid breadth.

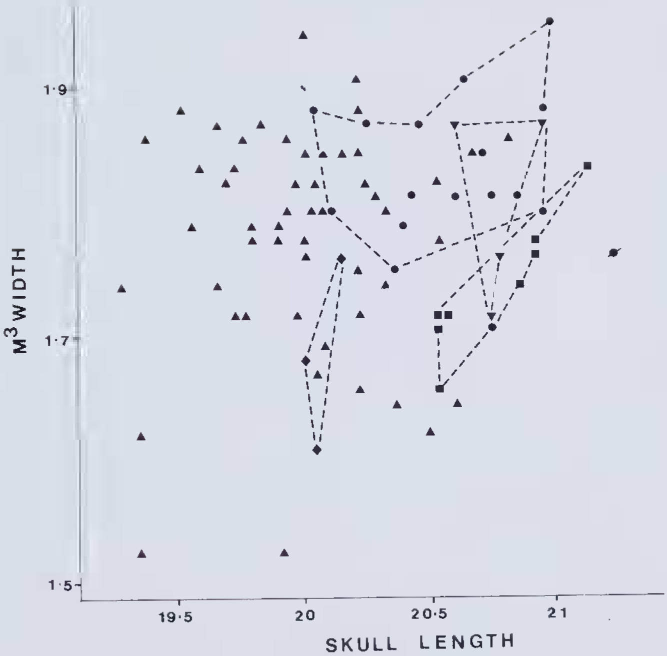


Figure 13 M^3 width *versus* greatest skull length.

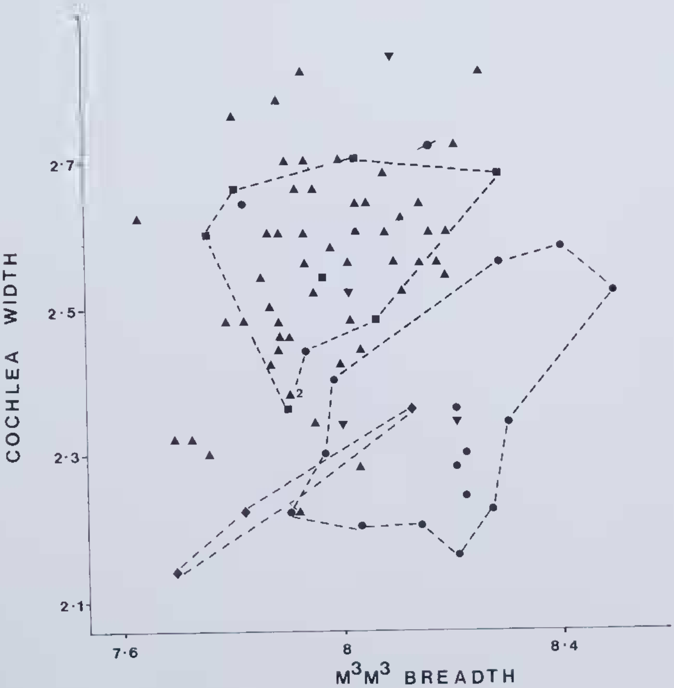


Figure 14 Cochlea width *versus* M^3M^3 breadth.

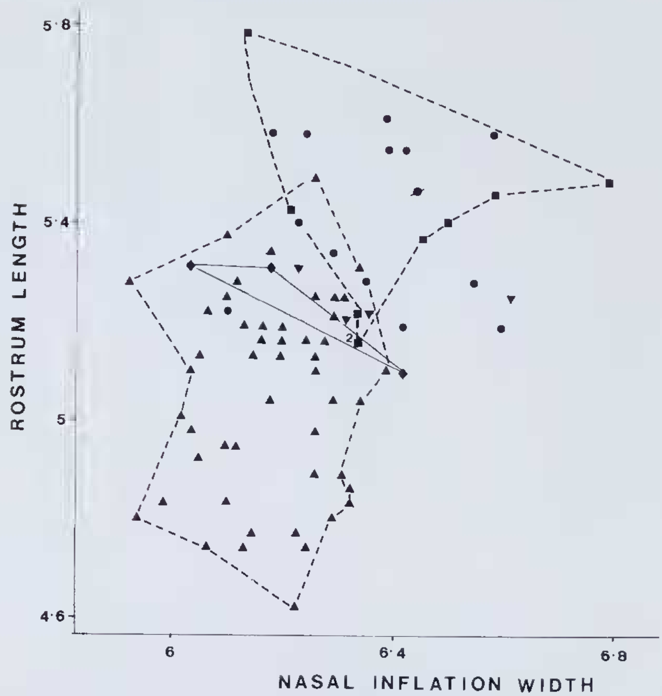


Figure 15 Rostrum length *versus* nasal inflation width.

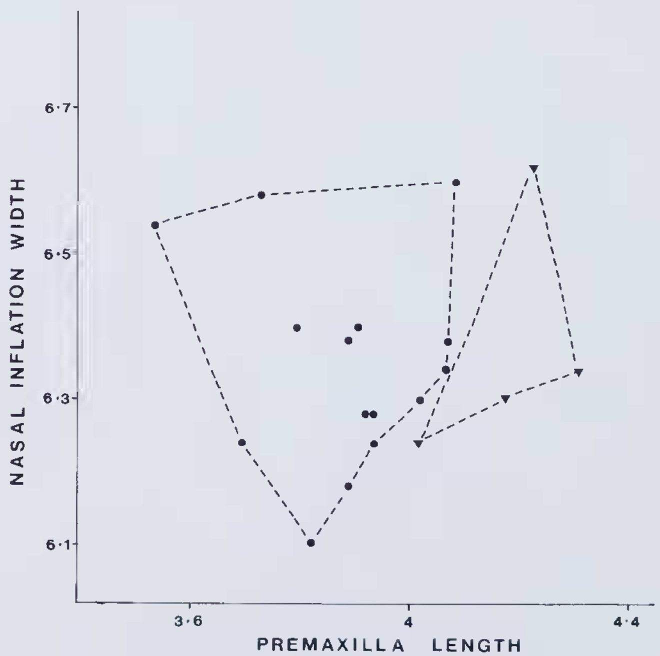


Figure 16 Nasal inflation width *versus* premaxilla length.

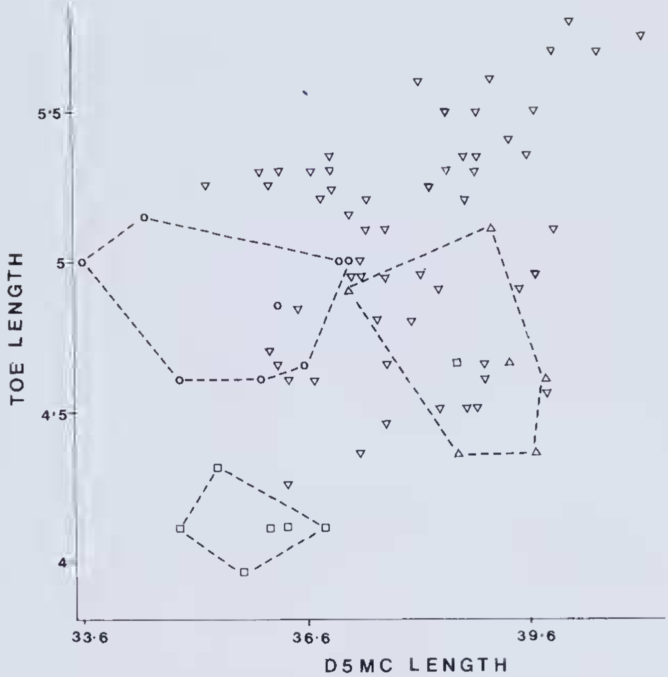


Figure 17 Toe length *versus* digit 5 metacarpal length.

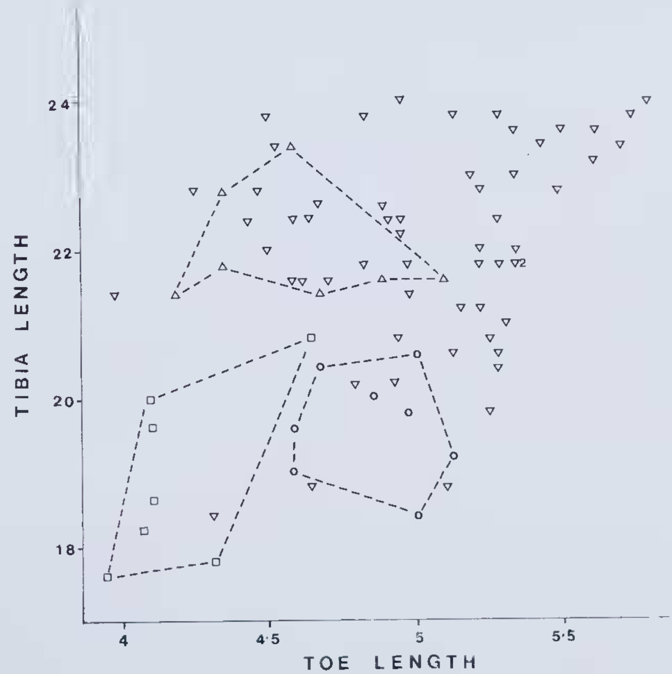


Figure 18 Tibia length *versus* toe length.

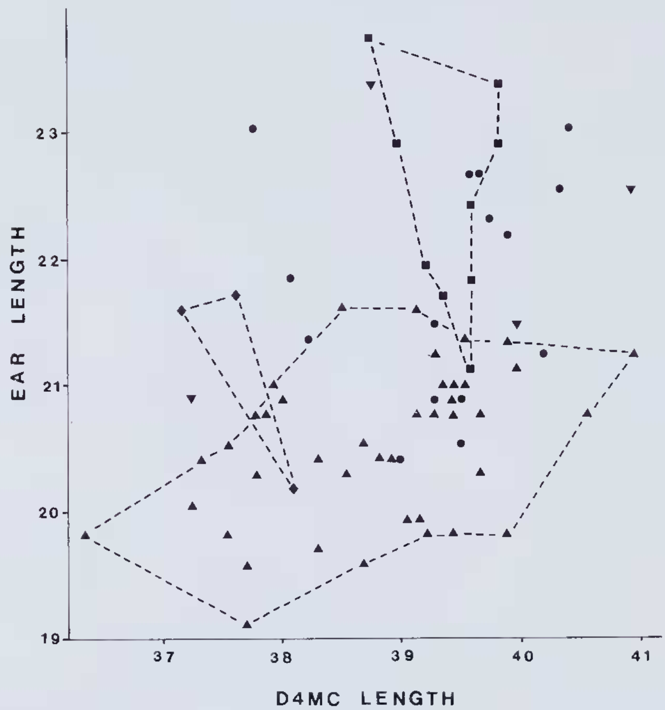


Figure 19 Ear length *versus* digit 4 metacarpal length.

Hipposideros sorenseni sp. nov.

Table 1; Figures 1,5d,7-9,17-18 and 22

Holotype

Museum Zoologicum Bogoriensis MZB 11333, skull separate, scientific 'cabinet' skin, collected by Bapak Sudarmanu on 15 January 1976.

Type locality

Gua Kramat (≡ holy cave), Pangandaran, W. Java (*c.* 7°41'S, 108°40'E).

Specimens examined

Listed in section "Specimens Examined".

Diagnosis

Hipposideros sorenseni skull generally similar in size to *H. larvatus*, but differs from that species in averaging smaller in both C^1C^1 breadth (5.34 v. 5.45) and dentary angle to condyle length (5.53 v. 5.87). Glans penis distally less laterally compressed and distal fleshy lobe attached to baculum more oval. Baculum more robust; dorsal profile suboval rather than long and thin with broad basal pedestal; bifurcating distal arms much shorter and robust.

It differs from *H. madurae* in having a generally larger skull. For example: greatest skull length (21.63 v. 20.84); braincase width (10.00 v. 9.50); zygomatic breadth (12.49 v. 12.23) and cranial length (14.43 v. 13.51); greatest skull length averages larger relative to nasal inflation length (3.808 v. 3.491); cranial length longer relative to nasal inflation length (2.541 v. 2.263); mastoid breadth wider relative to least interorbital width (Figure 7). Digit 5 metacarpal length longer relative to toe length (Figure 17); tibia length longer relative to toe length (Figure 18). Baculum longer (1.15-1.20 v. 0.75-0.93); distal bifurcating arms relative shorter with concomitant broader solid basal part.

It differs from *H. sumbae* in averaging larger in most skull measurements (Table 1). For example; greatest skull length (21.63 v. 20.24); palatal bridge length (3.82 v. 3.41); nasal inflation length (5.68 v. 5.18); nasal inflation width (6.48 v. 6.24); dentary length (14.92 v. 13.91); M^3M^3 breadth (8.66 v. 8.01); I_1M_3 length (10.03 v. 9.23); palatal width relatively broader as indicated by M^3M^3 breadth relative to nasal inflation width (Figure 8); nasal inflation length relative to nasal inflation width larger (0.877 v. 0.830) dentary length larger relative to rostrum length (Figure 9). Digit 5 phalanx 2 longer (10.91 v. 9.53-9.92). Glans penis with distal end lateral profile squarer. Baculum longer (1.15-1.20 v. 0.75-0.84), more robust, cranial projection of bifurcating arms with distal edge more vertical.

Description

Skull (Table 1, Figure 22)

Generally similar in size and description to that of *H. l. larvatus* but differs in both C^1C^1 breadth and dentary angle to condyle averaging smaller; supraorbital ridges slightly weaker; frontal depression very shallow; sphenorbital bridge slightly constricted posteriorly and only partially conceals sphenorbital sinus.

Externals

As for *H. l. larvatus.*

Glans penis

As for *H. m. madurae.*

Baculum (Figure 5d)

Large robust baculum with greatest length 1.15-1.20 (N= 2); base large, comprises approximately two-thirds length of baculum, width 0.64-0.65; bifurcating distal arms short with cranial height from base 0.59-0.65.

Distribution

Pangandaran, southern border of C. and W. Java (Figure 1).

Etymology

Named after Dr Kurt Sorensen, Officer in Charge, U.S. Naval Medical Research Unit No. 2, Jakarta Detachment, in recognition of his support and encouragement of staff of the Western Australian Museum/Museum Zoologicum Bogoriense with their research programme in Indonesia.

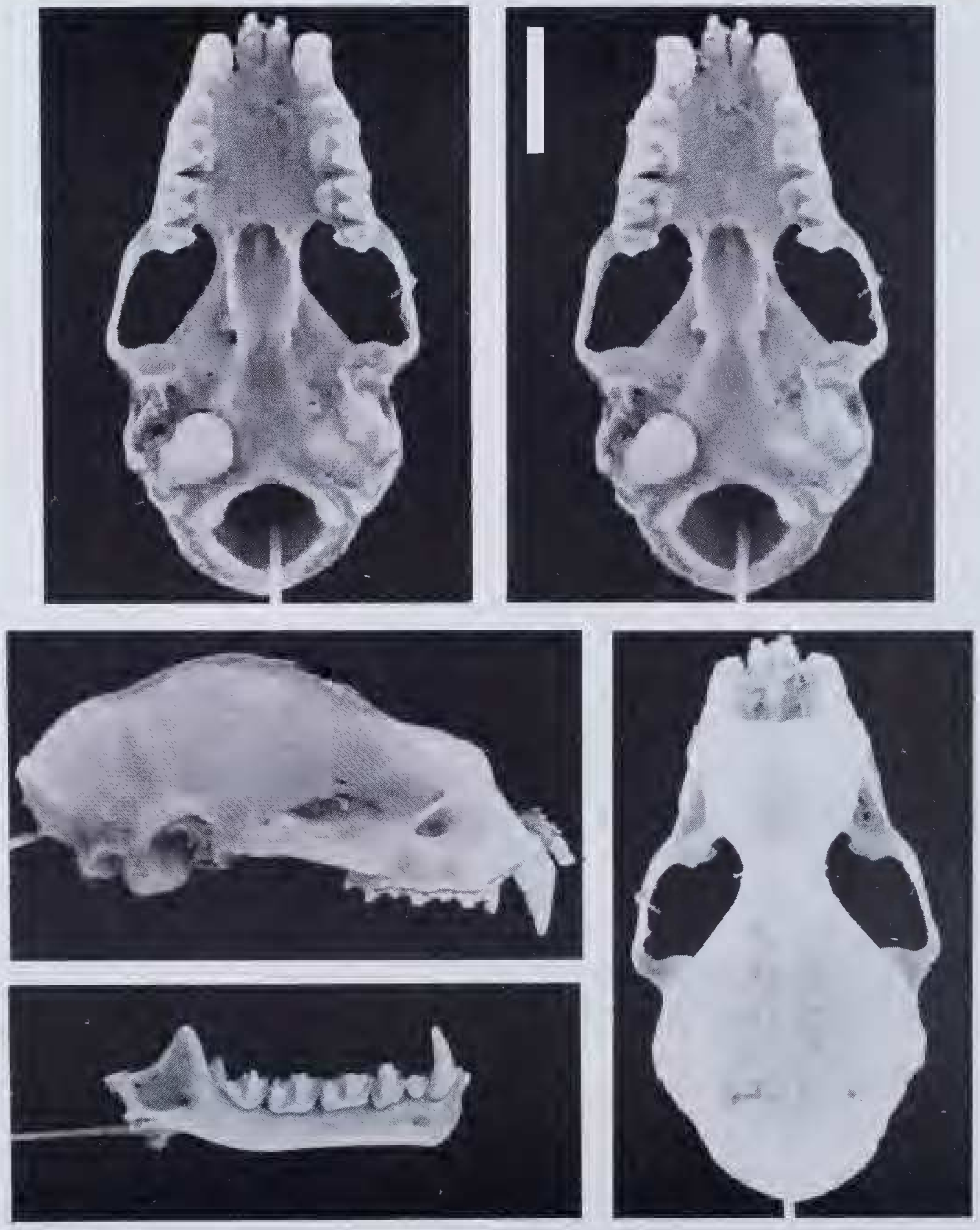


Figure 20 Photograph of skull and dentary of *Hipposideros m. madurae*, MZB 10613 B, holotype. Ventral view as stereopair; scale line 5 mm.

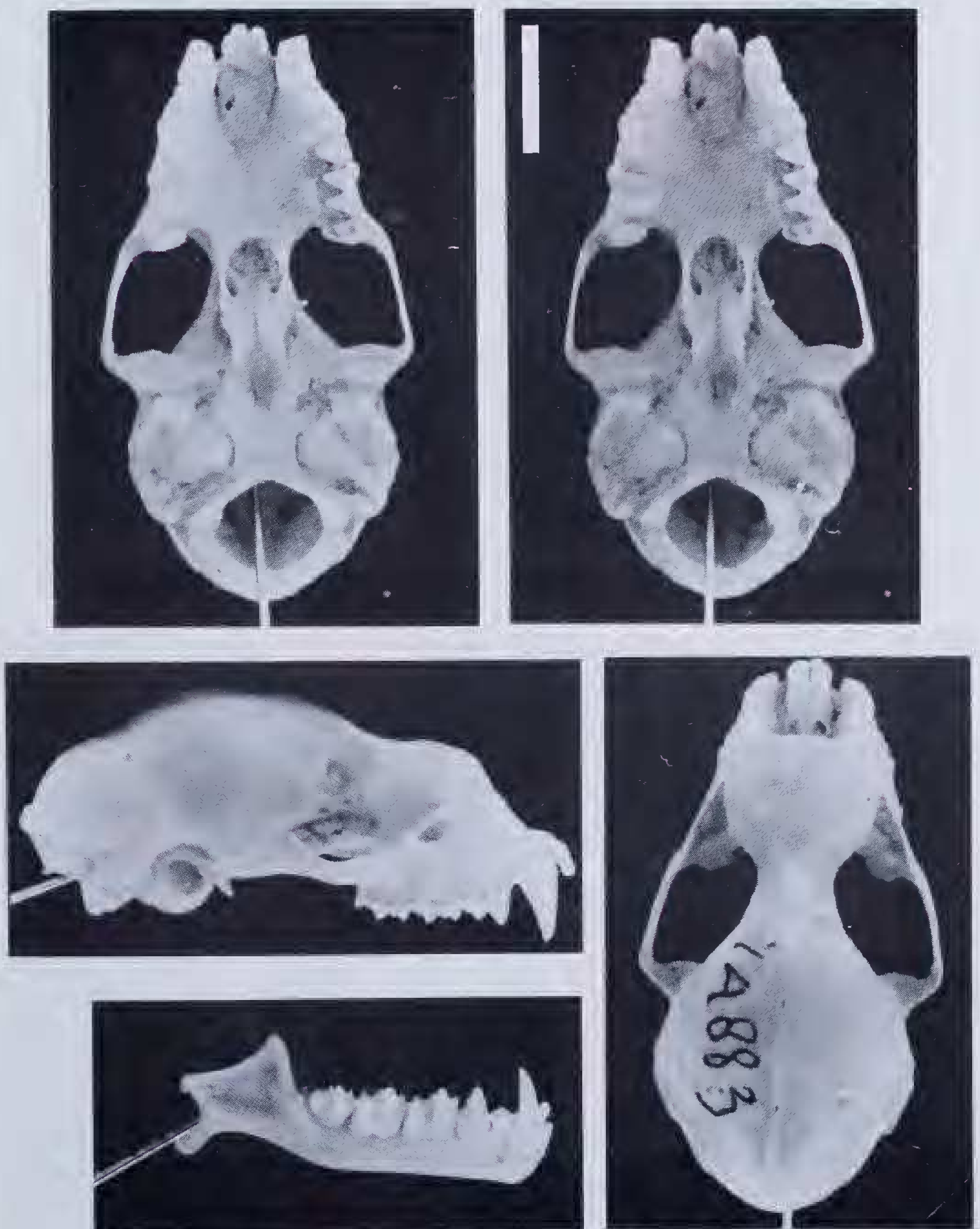


Figure 21 Photograph of skull and dentary of *Hipposideros m. jenningsi*, MZB 14883, holotype. Ventral view as stereopair; scale line 5 mm.

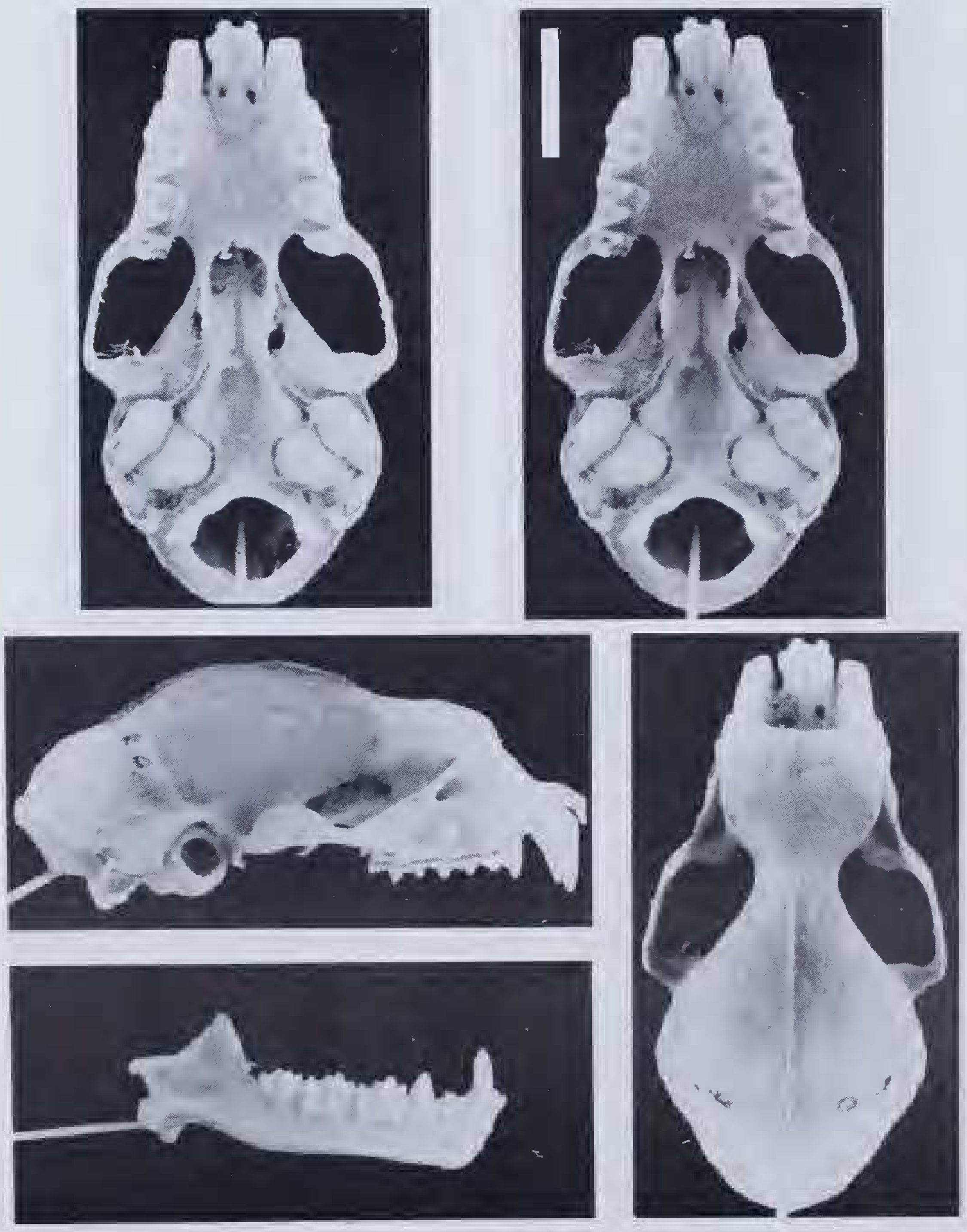


Figure 22 Photograph of skull and dentary of *Hipposideros sorenseni* MZB 11333, holotype. Ventral view as stereopairs; scale line 5 mm.

Figure 23 Photograph of skull and dentary of *Hipposideros s. sumbae* (WAM M30493) from Sumba I. Ventral view as stereopairs; scale line 5 mm.

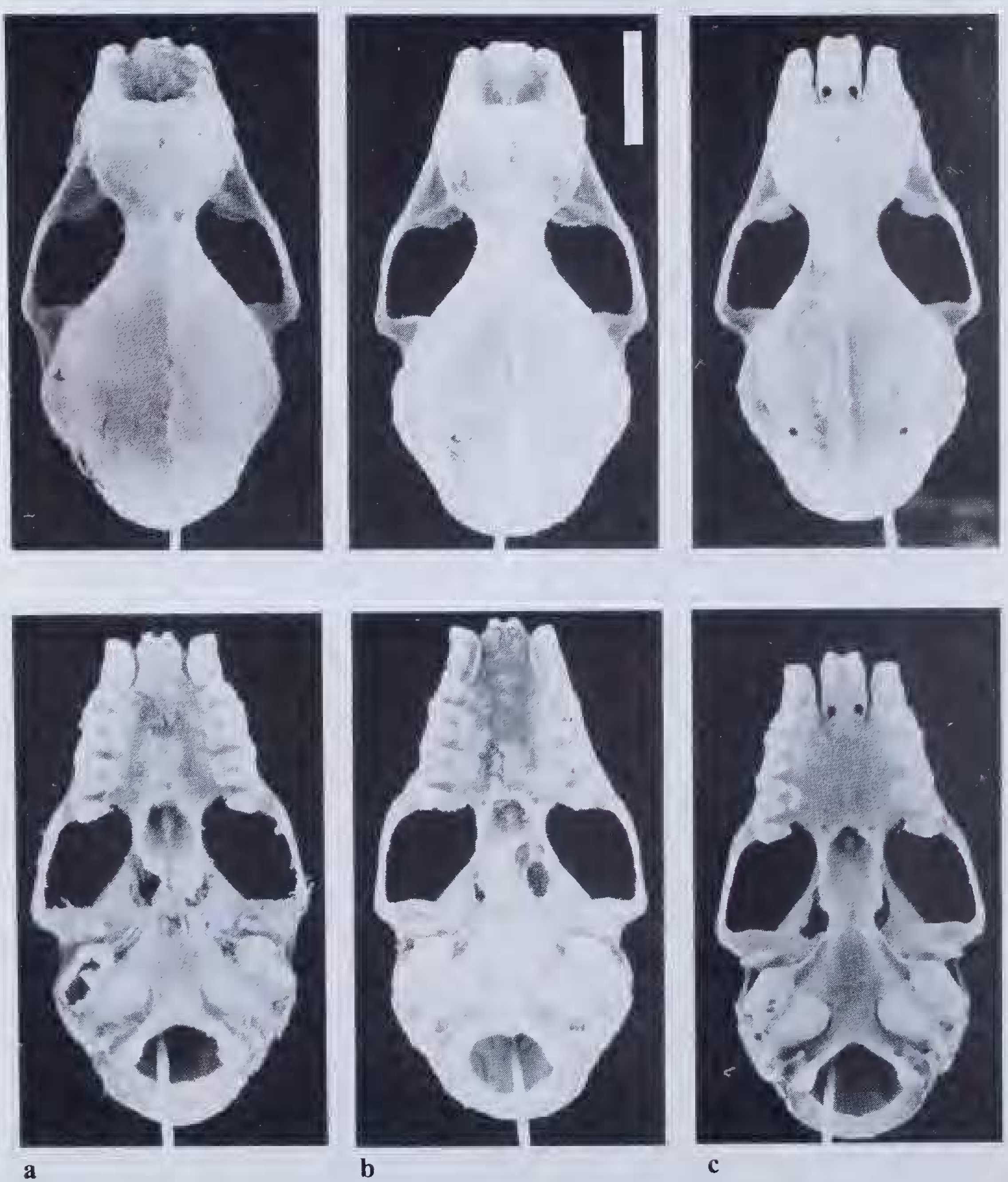
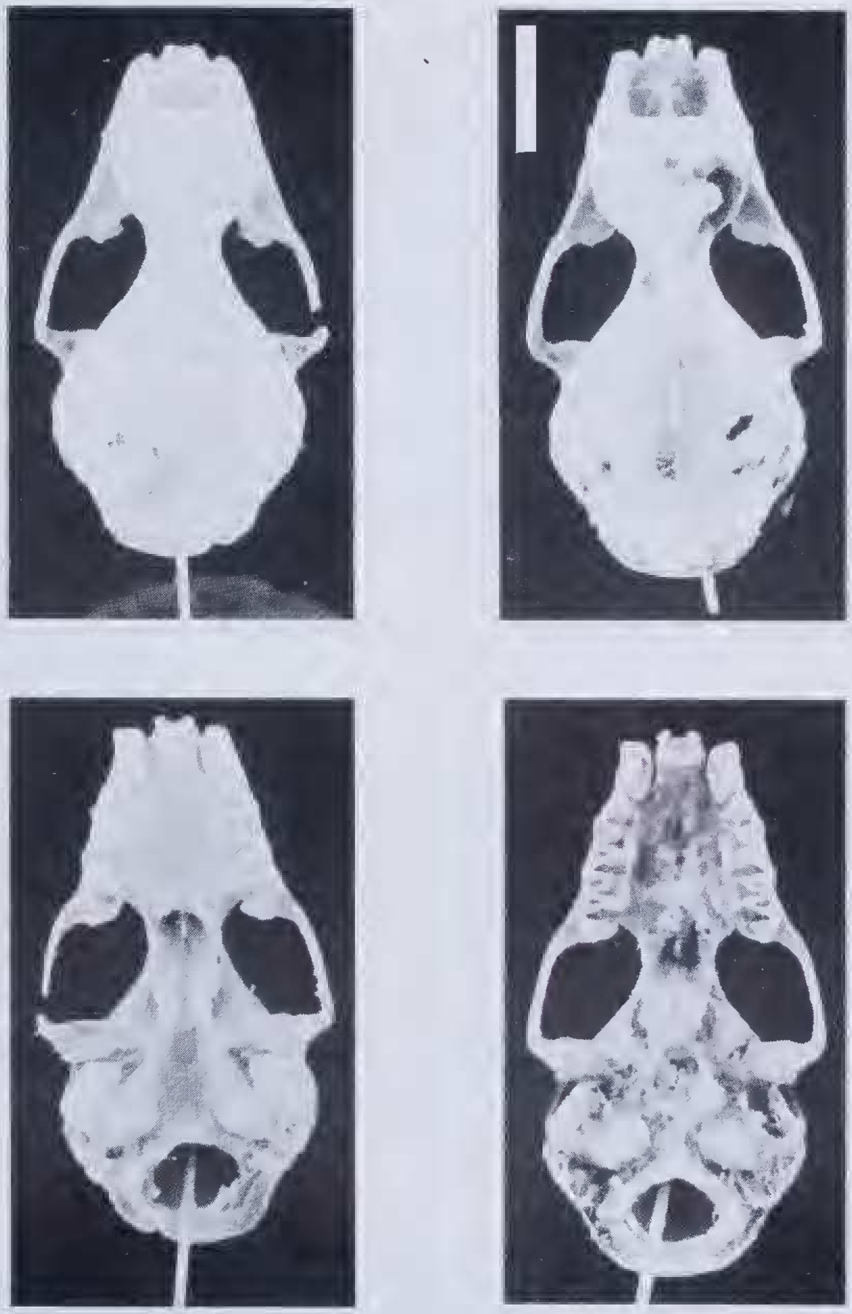


Figure 24 Photograph of skull of (**a**) *Hipposideros s. sumbae* (WAM M30493); (**b**) *H. s. rotiensis* (WAM M35436) and (**c**) *H. s. sumbawae* (WAM M31494); scale line 5 mm.



d

e

Figure 24 (cont). Photograph of skull of (**d**) *Hipposideros s.* subsp. indet. A (WAM M38016); and (**e**) *H. s.* subsp. indet. B (WAM M35213); scale line 5 mm.

Hipposideros sumbae Oei, 1960

Diagnosis

Hipposideros sumbae differs from *H. larvatus, H. madurae* and *H. sorenseni* in averaging smaller in most skull measurements (Table 1). Posterior palatal width relatively narrower as indicated by M^3M^3 breadth relative to nasal inflation width (Figure 8); nasal inflation length relative to nasal inflation width smaller (0.830 v. 0.877-0.960); dentary length smaller relative to rostrum length (Figure 9). Digit 5 phalanx 2 shorter (9.53-9.92 v. 10.44-10.91). Glans penis with distal end lateral profile more pointed.

Hipposideros sumbae sumbae Oei, 1960

Table 1, Figures 1,5e,6c,8-9,11-15 and 24a

Hipposideros larvatus sumbae Oei, H.P., 1960, Notes on bats from Bali, Lombok and Sumba. Hemera Zoa. 67: 28-31.

Lectotype

Naturhistorisches Museum Basel number 5651/10157, adult male, collected by the Sumba-Expedition Bühler-Sutter 1949. Lectotype designated by van Bree (1961). Lectotype skull illustrated in Oey and van der Feen (1958).

Type locality

E. Sumba, Nusa Tenggara, from cave (*c.* 9°55′S, 120°41′E).

Specimens examined

Listed in section "Specimens Examined".

Diagnosis

Hipposideros s. sumbae differs from *Hipposideros s. rotiensis* subsp. nov. in having a skull with premaxilla length absolutely narrower and also narrower relative to dentary length (Figure 11); cochlea width shorter relative to mastoid breadth (Figure 12) and M^3M^3 breadth (Figure 14). M^3 width larger relative to greatest skull length (Figure 13). Digit 3 phalanges 1 and 2 generally smaller (17.53 v. 18.36 and 17.77 v. 18.84, respectively).

It differs from *Hipposideros s. sumbawae* subsp. nov. in averaging larger in many skull characters (Table 1). For example, greatest skull length (20.57 v. 20.01), braincase width (9.68 v. 9.34), zygomatic breadth (12.12 v. 11.80), I_1M_3 length (9.40 v. 9.16); greatest skull length averages longer relative to cranial height (3.160 v. 3.074); cochlea width shorter relative to M^3M^3 breadth (Figure 14); rostrum generally shorter and nasal inflation generally narrower (Figure 15); and ear length averages larger (21.81 v. 20.51).

Description

Skull (Figure 24a)

Similar to *H. l. larvatus* except for the following: most skull measurements average smaller; posterior palatal width relatively narrower as indicated by M^3M^3 breadth relative to nasal inflation width (Figure 8); nasal inflation length relative to nasal inflation width smaller (0.830 v. 0.884); dentary length smaller relative to rostrum length (Figure 9); sagittal crest occasionally reaches lambdoidal crest; supraorbital ridges very weak; nasal inflation only slightly arched in lateral profile; posterior palatal emargination usually u shaped, occasionally with tiny median posterior projection; PM_2 length small, usually less than three-quarters PM_4 length.

Externals

As for *H.l. larvatus* but colour of pelage on lower back a darker Fuscous to Burnt Umber; shoulder and neck cape generally a larger area of paler fur than in *H. l. larvatus* and extends often to middle of back.

Glans penis (Figure 6c)

Distal outline of glans suboval, in lateral profile rod shaped with dorsolateral edge of distal end gently sloping and not projecting anteriorly as in other species considered; apical fleshy lobe attached to baculum suboval, elongate and sloping sharply into dorsal urethral groove, this lobe with two large suboval basal eminences.

Baculum (Figure 5e)

Short, greatest length 0.75-0.84 (2), suboval in dorsal outline; solid base greatest width 0.51 (2); distal bifurcating arms robust approximately half greatest length and with cranial height 0.41-0.42 (2) above base; distal arm cranial part subvertical.

Distribution

Sumba I., Nusa Tenggara, Indonesia.

Etymology

Named after Sumba I.

Hipposideros sumbae rotiensis subsp. nov.

Table 1, Figures 1,5f,11-15,19 and 24b

Holotype

Western Australian Museum number (WAM) M35436, adult male, carcase fixed in 10% formalin and preserved in 70% ethanol; liver in WAM ultrafreezer, skull separate. Capture in cave by D.J. Kitchener on 10 October 1990. Weight 13.0 gm.

Type locality

Sangoen, Roti I. (*c.* 10°43'S, 123°09'E), altitude 10 m, in deep narrow limestone cave, area vegetated with partly cleared very open mixed woodland.

Paratypes

See section "Specimens Examined".

Diagnosis

Hipposideros s. rotiensis differs from *Hipposideros s. sumbae* in the characters indicated above in the diagnosis of that subspecies.

It differs from *Hipposideros s. sumbawae* subsp. nov. in having a generally larger skull (Table 1). For example: greatest skull length (20.76 v. 20.01), braincase width (9.59 v. 9.34), nasal inflation width (6.40 v. 6.18), dentary length (14.10 v. 13.77); nasal inflation width and rostrum length larger (Figure 15); and ear larger (Figure 19).

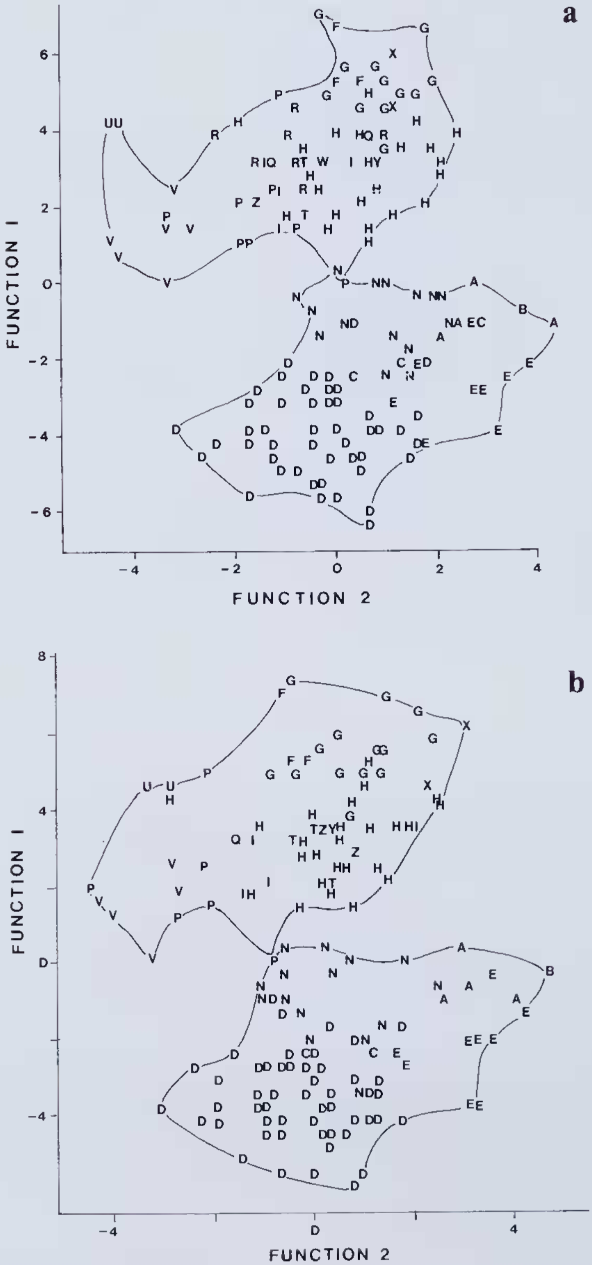


Figure 25 Canonical variate (discriminant) analysis plots of functions 1 and 2 for *Hipposideros* spp. considered in this study **grouped by localities** based on (a) skull and (b) external characters. Specimens group into two broad clusters: Nusa Tenggara (A, Semau I.; B, Timor I.; C, Savu I; D, Sumbawa I.; E, Roti I.; and N, Sumba I.) and 'Western' (F, Nias I.; G, Carita — W. Java; H, Krakatau Is; I, Ciampea — W. Java; P, Madura I.; Q, Pulau Laut — SC Java; R, Pangandaran — W/C Java; T, Aceh, N. Sumatra; U, Palembang — C. Sumatra; V, Semarang, C. Java; W, Sukabumi — W. Java; X, Cikajang — W. Java; Y, Ujong Kulon; Z, Candi — W. Java.

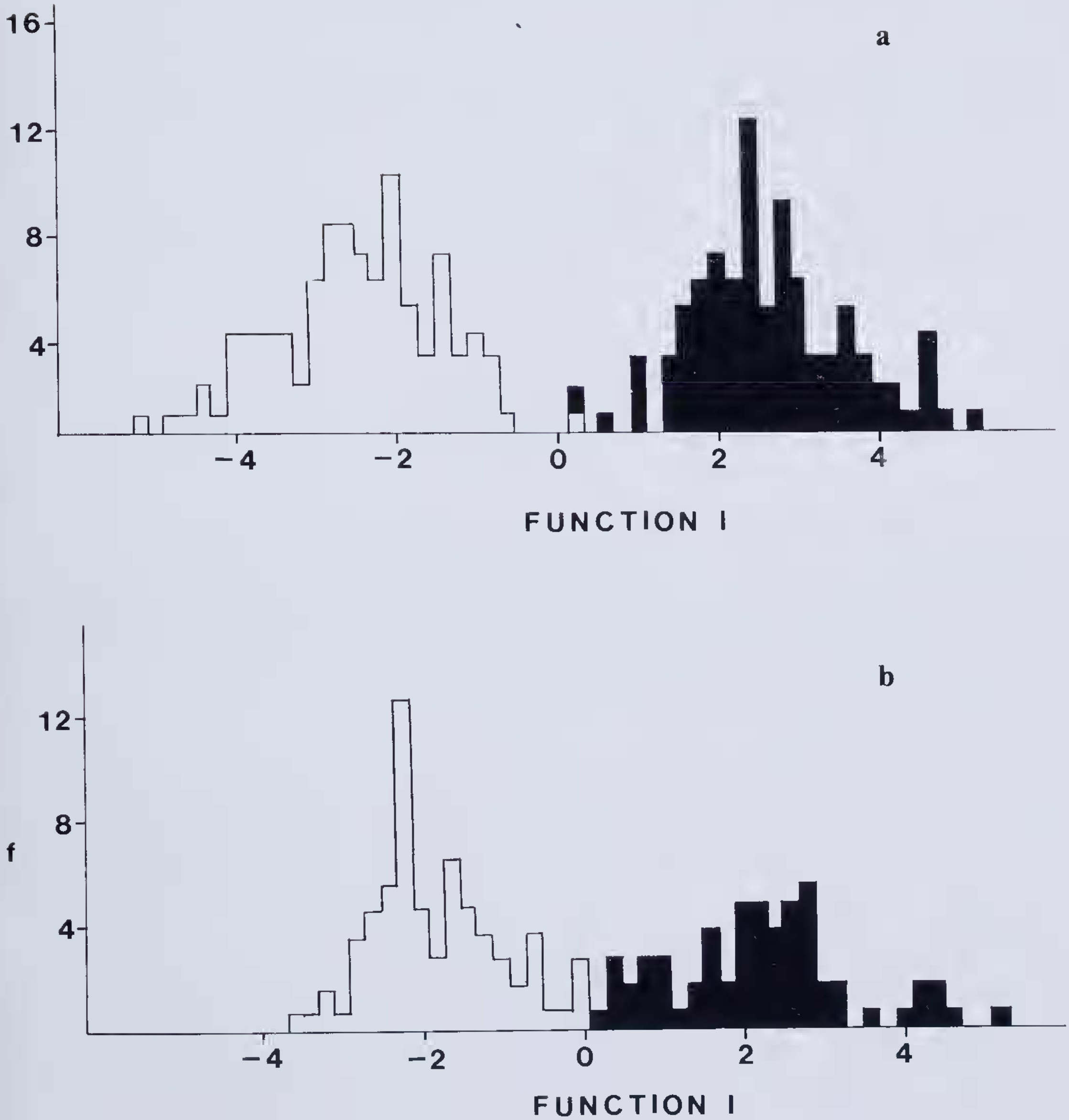


Figure 26 Canonical variate analysis of all specimens of *Hipposideros* spp examined but grouped into the Nusa Tenggara group and the Western group of Figure 25. Histogram of function 1 for (a) skull and (b) external characters □, Nusa Tenggara group and ■ Western group.

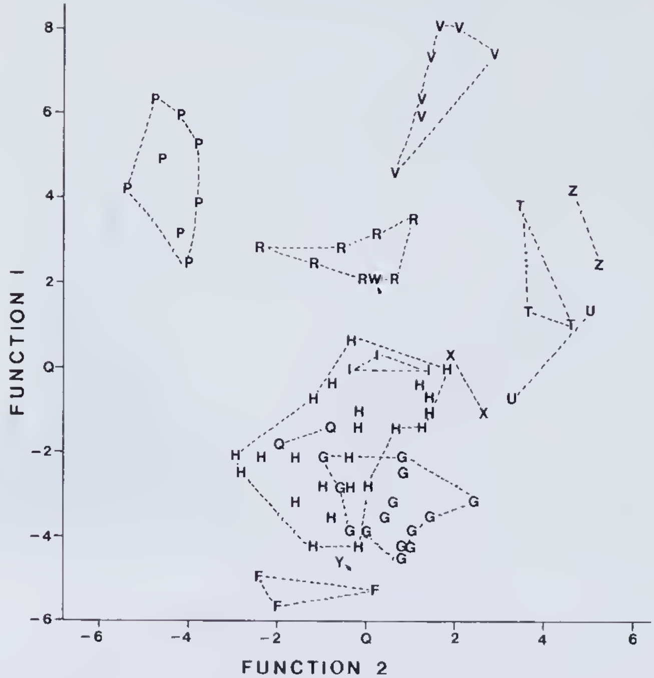


Figure 27 Canonical variate analysis based on skull characters of specimens of *Hipposideros* spp studied from the Western group of Figure 25, **grouped by collection locality**. Collection localities code as for Figure 25.

Description

Skull (Table 1, Figure 24b).

Externals, glans penis and baculum (Figure 5f) similar to *H. s. sumbae* but skull with cochlea longer (2.56 v. 2.32) and M^3 width smaller (1.73 v. 1.84); baculum similar in size and shape but with bifurcating distal arms tending to be wider apart, dimensions of baculum (N = 2): greatest length 0.76, basal width 0.55 and height above base of cranial part 0.32.

Distribution

Roti I., Nusa Tenggara, Indonesia (Figure 1).

Etymology

Named after Roti I.

Referred specimens

MZB 14852, adult male, puppet skin, skull separate, collected at Camplong, W. Timor on 6 January 1932. This specimen is referred to *H. sumbae rotiensis.* It exceeds the Rotinese specimens in some measurements. For example: mastoid breadth, rostrum height, cranial length, mesopterygoid foramen breadth, C^1C^1 breadth dentary length) but it lies closest to the Rotinese cluster in DFA (Figure 29). In particular it is placed in the Rotinese population in Figure 29c. This is a plot of functions 2 and 3 and would appear to be more influenced by shape rather than size differences.

Hipposideros sumbae sumbawae subsp., nov.

Table 1, Figures 1,5g,14,15,19 and 24c

Holotype

Western Australian Museum number (WAM) M31494, field number S383; adult male; weight 13.5 gm; carcase fixed in 10% formalin and preserved in 70% ethanol; liver in WAM ultrafreezer; skull separate; collected on 26 May 1988 in bat trap by D.J. Kitchener, R.A. How and Maharadatunkamsi.

Type locality

Gua (≡ cave) Batu Tering, 3 km S. Desa Batu Tering, W. Sumbawa, (*c.* 8°48′S, 117°22′E); from side adit of enormous limestone cavern; altitude *c.* 200 m. Stream passes within a few metres of cave, vegetation surrounding a dense gallery forest.

Paratypes

See section "Specimens Examined".

Diagnosis

Hipposideros s. sumbawae differs from both *H. s. sumbae* and *H. s. rotiensis* in the characters indicated above in the diagnoses of those subspecies.

Description

Skull (Table 1, Figure 24c), externals, glans penis and baculum (Figure 5g) similar to *H. s. sumbae* but skull with generally larger cochlea width (2.54 v. 2.32), rostrum length smaller (5.04 v. 5.39) and nasal inflation length smaller (5.11 v. 5.30). Baculum similar in size and shape: greatest length 0.83 ± 0.020 (3), basal width 0.49 ± 0.012 (3) and height above base of cranial part 0.33 ± 0.043 (3), slope of anterior edge of cranial projecting part of distal arms varies from near vertical to sharply sloping posteriorly (Figure 5g).

Distribution

Sumbawa I. and Flores I., Nusa Tenggara.

Etymology

Named after Sumbawa I.

Referred specimen

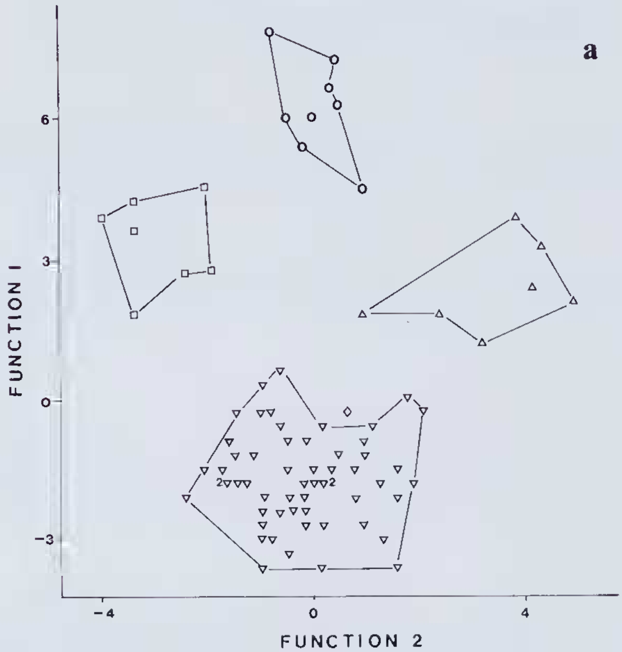
MZB 14243, ♂, skin and skull, from Gua Cermin near Labuan Bajo, W. Flores. This specimen had an injury to its right dentary which has repaired but left considerable bone damage and ossification. Its skull development is also likely to have been impaired as a consequence of this injury. For this reason it was not included in the analyses. However, inclusion of this specimen in the DFA placed it as an outlier of the Sumbawa population. The senior author visited this large cave in April 1990; no *Hipposideros* were present.

Hipposideros sumbae subsp. indet. A.

Table 1, Figures 1,5h,16,24d

Skull (Figure 24d)

The four specimens from **Semau I.** (see "Specimens Examined") appear to represent a distinct form. They have a distinct skull shape as shown by the plot of DFA functions 2 and 3 (Figure 29b). These specimens when unallocated in the DFA, classified into the



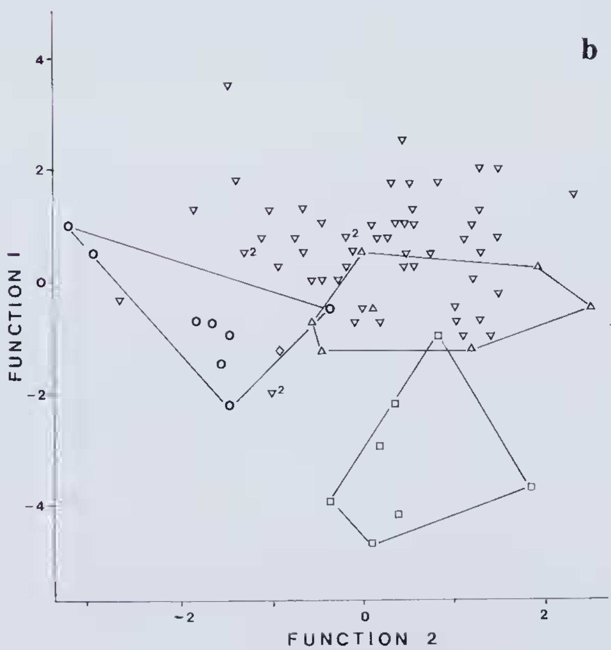


Figure 28 Canonical variate analysis based on skull characters of specimens of *Hipposideros* spp from the Western Group of Figure 25 **grouped by taxa** (*H. l. larvatus; H. m. madurae; H. m. jenningsi; H. sorenseni* and *H.* sp. indet. (Sukabumi — unallocated) **(a)** skull and **(b)** external characters.

Roti, Sumba and Sumbawa groups (see earlier). Most of their measurements overlap with those of other *H. sumbae* forms. This form can be distinguished from *H. s. sumbae* by having a larger premaxillae length relative to its nasal inflation width (Figure 16) and longer premaxillary length relative to nasal inflation width (0.656 v. 0.611) and digit 3 phalanx 1 averages larger (18.47 v. 17.85). Compared to *H. s. rotiensis* it has a wider M^3 width relative to rostrum length (0.434 v. 0.403) and rostrum length narrower relative to greatest skull length (0.253 v. 0.260). Compared to *H. s. sumbawae* its skull is generally larger (Table 1). For example, greatest skull length (20.78 v. 20.01), braincase width (12.15 v. 11.80), dentary length (14.24 v. 13.77) and greatest skull length generally longer relative to cranial height (3.142 v. 3.074); ear generally longer (22.06 v. 20.51); *H. sumbae* subsp. indet. A is distinct from *H. sumbae* subsp. indet. B (from Savu Island) in having skull generally larger (Table 1). For example, greatest skull length (20.78 v. 20.08); braincase width (9.72 v. 9.05). Least interorbital width relative to greatest skull length smaller (0.142 v. 0.153).

Externals

Glans penis and baculum

The glans penis and baculum (Figure 5h) are very similar to the other forms of *H. sumbae*. The baculum examined had the dimension: greatest length 0.86; greatest width 0.52; and height of cranial part of distal arm above base 0.41. The anterior face of this cranial part almost vertical.

***Hipposideros sumbae* subsp. indet. B**

(Table 1, Figures 1,5c,13,14 and 24e)

Skull (Figure 24e)

The three specimens from **Savu I.** (see "Specimens Examined") cluster separately in discriminant function space from the other forms of *H. sumbae* (Figure 29a,b). They appear to represent a distinct form from these other subspecies from which they may be distinguished as follows:

It differs from *H. s. sumbae* by having a smaller skull (Table 1). For example, greatest skull length (20.08 v. 20.57); braincase width (9.05 v. 9.68); zygomatic breadth (11.57 v. 12.12); M^1 width (1.88 v. 2.06); I_1M_3 length (9.19 v. 9.40); M^3 width smaller relative to greatest skull length (Figure 13); and mastoid breadth narrower relative to mesopterygoid width (2.519 v. 2.704).

It differs from *H. s. rotiensis* in having a much smaller skull (Table 1). For example, greatest skull length (20.08 v. 20.76); braincase width (9.05 v. 9.59); dentary length (13.79 v. 14.10); greatest skull length smaller relative to M^3 width (Figure 13) and cranial height (3.142 v. 3.160); braincase width smaller relative to mastoid breadth (0.887 v. 0.923); cochlea width smaller relative to M^3M^3 breadth (Figure 14) and digit 4 metacarpal smaller (37.67 v. 39.44).

It differs from *H. s. sumbawae* in having cochlea width smaller relative to M^3M^3 breadth (Figure 14).

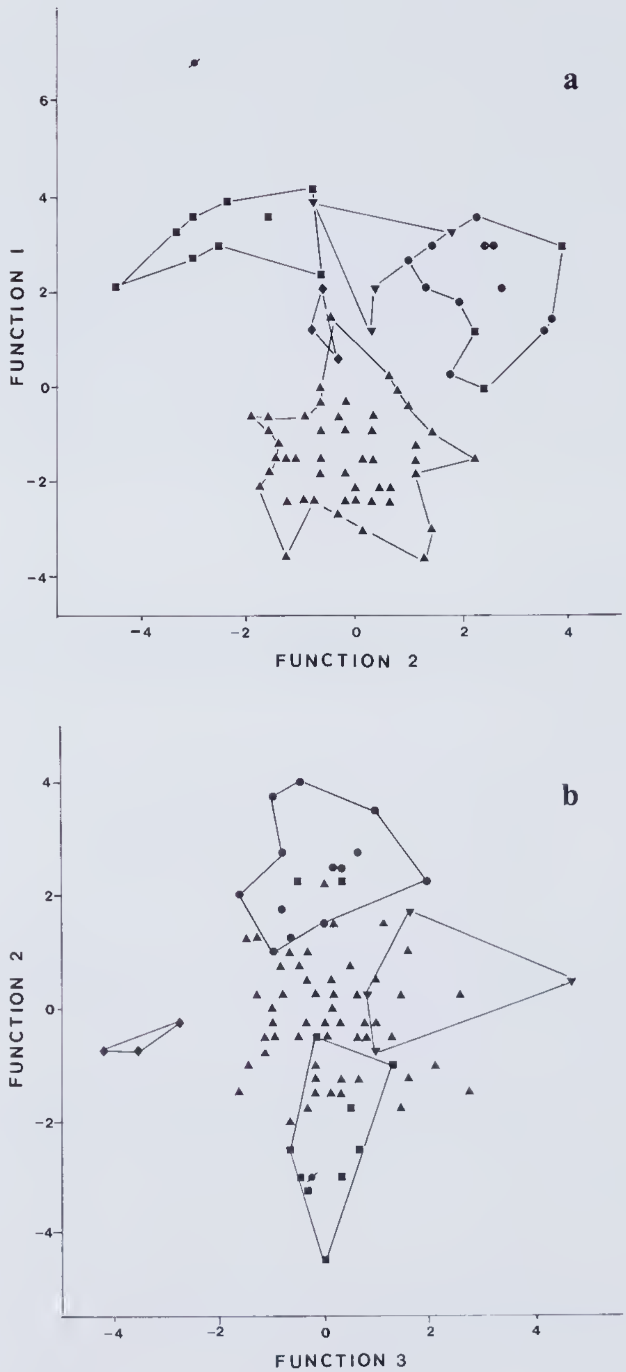


Figure 29 Canonical variate analysis of specimens from Nusa Tenggara **grouped by island**, based on skull characters (**a**, plot of functions 1 and 2; **b**, plot of functions 2 and 3) and (**c**) external characters, plot of functions 1 and 2 group. Island locality codes as for Figure 7.

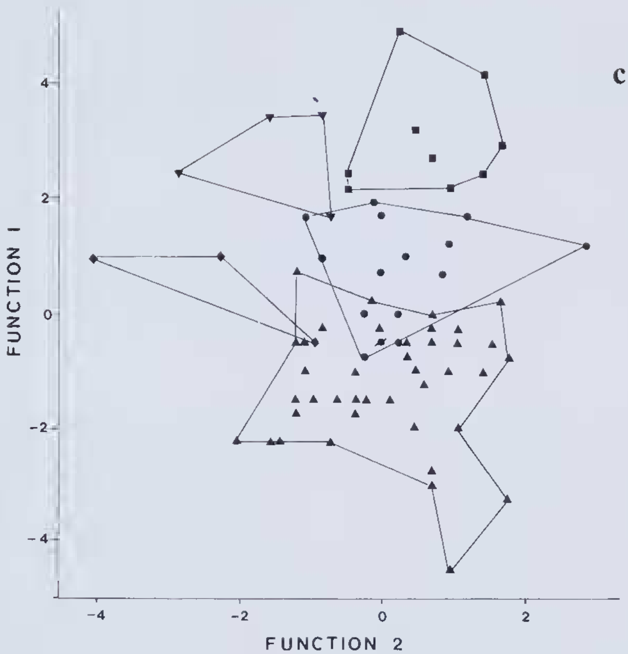


Figure 29 (cont).

It differs from *H. sumbae* subsp. indet. A in having skull generally smaller (Table 1). For example, greatest skull length (20.08 v. 20.78); braincase width (9.05 v. 9.72). Least interorbital width relative to greatest skull length greater (0.153 v. 0.142).

Externals

Glans penis and baculum

The glans penis and baculum (Figure 5i) very similar to other forms of *H. sumbae*. The baculum examined had dimensions: greatest length 0.80; greatest width 0.53; and height of cranial part of distal arm above base 0.43; anterior face of this cranial part almost vertical.

***Hipposideros* sp. indet.**

WAM M30008-09, a male and female from Gua Cidolog, Cikopeah, near Sukabumi. On skull characters the female specimen was close to the *H. larvatus* group, whereas on external characters it was closest to *H. m. madurae* (Table 1, Figure28a,b). The male had missing values and was not included in the analysis. Glans penis similar to *H. madurae* and *H. sorenseni* but its baculum is a unique shape (see Figure 5j); while most similar to bacula from *H. l. larvatus* specimens from Krakatau Is, Ujong Kulon, Nias I. etc., its basal part differs considerably in shape. Rather than a squat short baculum base in dorsal profile, it is narrowed and rounded with greatest width at a point approximately one-third the greatest length rather at the most proximal part. Its dimensions are as follows: greatest length 1.15; greatest width 0.53; height of cranial part of distal bifurcating arm from its base 0.50.

Results and Discussion

(1) Univariate Statistics

Mean, standard deviation, maximum, minimum values and sample size of each taxon are presented in Table 1 for (a) skull and (b) external characters.

(2) Multiple Regression

A multiple regression of skull and external characters on sex, age (young adult, adult, mature adult) and locality groups reflecting species (*Hipposideros madurae, H. sorenseni, H. larvatus* and *H. sumbae*). The results of these analyses are presented in Table 2. The effects and interactions are discussed below.

Skull

Sex: Only nasal length (N1L) and M^3 width (M^3W) showed a significant relationship with sex alone ($P = 0.028$ and $P = 0.035$, respectively). However, there was a significant interaction between sex and age for cranial length (P1L) ($P = 0.003$) and between sex and species for rostrum height (RH) ($P = 0.035$), M^3M^3 breadth (M^3M^3B) ($P = 0.034$), C^1 width ($P = 0.036$) and M^2 length (M^2L) ($P = 0.048$). These characters are related to dentition, width of palate, robustness of rostrum and cranial length. These may relate to functional relationship concerned with masticating power but more likely these significant relationships are due to chance. This is because six of the seven significant relationships had a low significance ($P>0.01$) and given the large number interactions being tested (124) about 6 such interactions could be expected to be significant by chance alone. Only the interaction between age and sex for cranial length was highly significant ($P = 0.003$).

Age: Only M^1 length showed a simple and significant relationship with age ($P = 0.005$, respectively). However, there was a significant interactive relationship for cranial length between sex and age (discussed above) and for both rostrum length (RL) and cranial length between age and species ($P = 0.013$ and 0.012, respectively). These significant relationships again probably resulted from chance alone.

Species: All but one of 31 skull characters (cochlea width) differed significantly between the species — most of them were highly significant. These differences were generally similar between the sex and age grouping considered, although there were significant interactions between species and sex for: rostrum height (RH) ($P = 0.035$), M^3M^3 breadth (M^3M^3B) ($P = 0.034$), C^1 width (C^1W) ($P = 0.036$) and M^2 length (M^2L) ($P = 0.048$) and between species and age for rostrum length (RL) ($P = 0.013$) and cranial length (P1L) ($P = 0.012$).

Externals

Sex: Digit 3 and 5, phalanx 1 length (D3P1, D5P1) showed a simple and significant relationship with sex ($P = 0.004$ and $P = 0.006$, respectively); with Digit 3 phalanx 1 there was also a significant interaction between sex and or age and species ($0.05 < P < 0.01$). These interactions resulted from the fact that females generally had a longer digit 3 phalanx 1 than males, but that in *H. larvatus* this was not the case, because for example, mature male had longer digit 3 phalanx 1 than mature females [19.08 (N=8) v. 18.84 (N=7);

Table 2 Multiple regressions on species of *Hipposideros (larvatus, sorenseni, madurae,* and *sumbae),* sex and age, based on skull and external characters. F values are presented for the basic effects and their interactions, significance levels are: *, 0.05> P> 0.01; **, 0.01> P> 0.001; and ***, P< 0.001.

	Main Effects			Interactions			
Character	Sex	Age	Species	Sex. Age. Species	Sex. Age	Sex. Species	Age. Species
GSL	0.050	0.031	77.327***	0.968	1.039	1.152	0.969
BW	0.263	0.918	54.140***	0.720	0.104	1.761	0.292
ZB	0.712	0.910	113.172***	1.615	0.648	1.954	0.578
MB	0.036	0.808	123.333***	0.612	0.402	1.979	0.965
CH	0.657	0.973	41.214***	0.512	1.189	0.454	1.136
RH	0.413	0.180	5.087**	1.260	1.725	2.956*	1.721
RL	3.624	1.604	3.496*	1.511	0.829	2.301	2.823*
LIOW	0.175	0.044	4.447**	0.536	1.571	0.310	0.579
PIL	2.101	3.931*	38.836***	2.223	5.927**	0.607	2.851*
NIL	4.938*	1.208	60.025***	0.762	0.113	2.528	0.704
PBL	2.113	1.141	37.758***	1.742	1.441	1.453	0.950
PML	1.093	2.987	9.501***	1.200	0.594	0.622	1.099
MF	0.111	0.054	6.681***	0.257	0.177	1.673	0.284
TBL	0.011	0.756	4.526**	1.882	1.323	0.540	1.246
TBB	0.100	0.049	84.956***	1.010	0.197	1.952	0.761
NIW	2.817	0.678	37.297***	0.801	0.575	2.017	0.768
CW	0.042	1.300	1.455	0.321	0.031	1.133	0.772
M^3M^3B	1.184	0.435	179.744***	0.403	1.601	2.979*	1.556
C^1C^1B	0.220	0.694	73.903***	0.606	1.785	1.788	0.827
C^1W	0.000	2.420	27.166***	0.962	1.436	2.917*	0.594
P^3L	0.148	0.170	17.428***	1.084	0.648	0.840	0.154
P^3W	0.013	0.581	38.027***	0.750	1.763	1.814	0.481
M^1L	0.014	5.604**	18.124***	1.852	0.967	0.076	0.855
M^1W	0.426	0.116	21.220***	1.128	0.534	0.521	0.599
M^2L	0.335	1.651	18.914***	0.322	0.219	2.702*	1.188
M^2W	0.178	0.108	19.295***	0.166	0.040	1.752	0.845
M^3L	3.052	2.610	21.653***	0.811	0.280	0.549	1.904
M^3W	4.510*	2.061	25.499***	0.335	0.404	1.622	0.848
I_1M_3L	0.107	0.231	106.295***	0.188	2.403	2.155	0.759
DL	0.182	0.204	141.044***	0.214	0.236	0.509	0.749
RAP	0.238	0.621	16.053***	1.804	0.114	0.103	0.519
SVL	0.566	1.273	21.841***	0.753	0.274	0.949	0.453
TVL	0.742	1.080	10.109***	1.804	3.160*	1.287	1.257
EL	0.067	1.755	1.499	0.710	0.263	0.628	0.785
TIL	0.096	0.251	58.231***	0.716	0.130	0.675	0.731
TOL	1.831	0.964	10.278***	0.397	1.079	2.455	2.082
FA	0.924	0.954	49.631***	1.901	1.645	0.999	1.316
D2MC	0.091	0.029	32.602***	0.364	1.938	1.184	1.346
D3MC	0.812	0.021	36.335***	0.713	2.050	0.700	1.124
D3P1	8.480**	2.904	29.678***	2.463*	3.797*	3.205*	1.144
D3P2	0.896	1.196	22.751***	0.290	0.273	0.923	0.688
D4MC	1.865	1.083	50.618***	0.209	1.139	1.138	0.844
D4P1	2.411	0.542	9.824***	0.289	0.527	2.774	1.757
D4P2	0.207	0.012	27.042***	0.619	0.067	0.267	0.954
D5MC	0.240	0.333	1.399***	0.817	1.452	1.029	1.249
D5P1	7.800**	2.332	9.823***	1.573	1.135	3.872	1.157
D5P2	0.498	0.015	34.280***	0.243	0.047	1.354	0.364

respectively]. Also adult females had longer digit 3 phalanx 1 than other age groups, but only in *H. madurae* and *H. larvatus.* There was also a weakly significant interaction between sex and age for the character tail to vent length (TVL) ($P = 0.046$).

Age: No characters were significantly influenced by age alone. However, tail to vent length showed a weak interaction between age and sex and as discussed above digit 3 phalanx 1 showed weakly significant interactions between age and/or sex and species.

Species: All external characters showed highly significant ($P<.001$) differences between the species, except for ear length (EL). Nearly all these differences were the same between sex and age grouping except for those discussed above (digit 3 phalanx 1 length and ear length).

(3) **Multivariate analysis**

Canonical variate (discriminant) analyses (DFA) was carried out on locality and taxonomic groupings using all 47 characters measured. Both sexes and age groups were combined in the following analysis. However, all these analyses were also carried out after deleting those characters shown in the multiple regression analyses to be significantly influenced by sex or age, despite the probability that these significant relationships may have resulted from chance alone. The deletion of these characters had little or no effect on the analyses or the conclusions. For this reason the results presented are from the analysis of the full character set.

All localities separate

The DFA of skull and external characters analysed separately produced two broad locality groups as shown by the plot of functions 1 and 2 (Figures 25a,b, respectively. These two groups, which are entirely separate on function 1, are (i) Nusa Tenggara and (ii) Madura, Java, Sumatra and associated islands (≡ Western group). Within these two broad groups are further distinct locality clusters.

Nusa Tenggara and Western groups

The DFA based on skull characters of specimens placed in the Nusa Tenggara or Western group extracted a single function with 99.5% of all cases allocated to their correct group (Figure 26a).

The characters that load heaviest on function 1 are (listed in decreasing order): M^3M^3 breadth (M^3M^3B), greatest skull length (GSL) and dentary length (DL) (see Table 3a). A stepwise discriminant analysis revealed that I_1M_3 length (I_1M_3L), nasal inflation length (NIL), palatal bridge length (PBL), rostrum length (RL) and nasal inflation width (NIW) were also important discriminants. These characters indicate that overall skull size, palatal width, shape of nasal inflation, length of rostrum and length of toothrows are important discriminants between the Nusa Tenggara and Western groups.

The DFA, based on external characters (this excludes *H. m. jenningsi*), for the Nusa Tenggara and Western groups extracted a single function (Figure 26b), with 100% of all cases correctly classified to the 'Nusa Tenggara' or 'Western' groups.

The characters loading heaviest on this function were digit 5 phalanx 1 length (D5P1), digit 3 phalanx 1 length (D3P1) and ear length (EL) (Table 3b).

Table 3 Canonical variate function coefficients for the Nusa Tenggara group and the Western group (Madura I., Java, Sumatra and associated islands) of *Hipposideros* specimens studied. Standardised values followed by (in brackets) unstandardised values (**a**) skull and (**b**) external characters.

(a)

Character	Function 1
GSL	—0.5994 (—1.1995)
BW	—0.3898 (—1.3072)
MB	0.3396 (1.4175)
RL	—0.1904 (—0.7726)
LIOW	—0.1186 (—0.6584)
PIL	0.3049 (0.7456)
NIL	0.3800 (1.2236)
PBL	0.3540 (1.7855)
NIW	—0.2777 (—1.6030)
M^3M^3B	0.7966 (4.4713)
C^1C^1B	—0.2379 (—1.0768)
P^3L	0.1213 (1.2764)
M^1W	0.1204 (0.9231)
M^2W	0.1384 (1.0702)
M^3L	0.1316 (2.6600)
M^3W	—0.1805 (—2.2049)
I_1M_3L	0.1924 (0.8058)
DL	0.5272 (1.3977)
Constant	—49.3789
Variance explained (%)	100

(b)

Character	Function 1
SVL	0.3832 (0.1597)
TVL	0.1429 (0.0604)
EL	—0.5383 (—0.5008)
TIL	0.2780 (0.2454)
FA	0.2337 (0.1386)
D3P1	0.5565 (0.6767)
D4MC	0.3326 (0.2397)
D4P1	—0.4993 (—0.8120)
D5MC	0.3125 (0.2533)
D5P1	—0.7281 (—1.1896)
D5P2	0.4754 (0.8730)
Constant	—24.7993
Variance explained (%)	100

Table 4 Canonical variate function coefficients for the first three functions for the Western group taxa (*H. l. larvatus; H. m. madurae; H. m. jenningsi; H. sorenseni*); standardised values followed by (in brackets) unstandardised values. (**a**) skull and (**b**) external characters.

(a)

Character	Function 1	Function 2	Function 3
GSL	0.8109 (1.6654)	0.5457 (1.1209)	—0.1452 (—0.2983)
BW	—0.1167 (— 0.4114)	0.5014 (1.7677)	—0.2290 (—0.8072)
MB	—0.6901 (— 3.4196)	0.4169 (2.0657)	0.3551 (1.7593)
CH	—0.6126 (— 2.9179)	0.0115 (0.0546)	0.2570 (1.2242)
RH	0.2455 (1.0785)	—0.1109 (—0.4873)	0.0265 (4.5103)
LIOW	0.4032 (2.3477)	—0.6334 (—3.6880)	—0.0039 (—0.0230)
PIL	0.3517 (0.8099)	0.7697 (1.7727)	—0.0942 (—0.2170)
NIL	0.6827 (1.9649)	0.2663 (0.7665)	—0.7248 (—2.0862)
PBL	0.6197 (2.8994)	0.0835 (0.3906)	0.0357 (0.1672)
PML	0.5573 (2.9408)	0.1476 (0.7791)	—0.4238 (—2.2365)
TBB	—0.7980 (— 3.3246)	—0.4145 (—1.7267)	0.2111 (0.8793)
NIW	—0.1326 (— 0.9113)	0.2735 (1.8796)	—0.3201 (—2.2002)
CW	—0.2990 (— 1.8797)	—0.5755 (—3.6181)	0.0386 (0.2426)
M^3M^3B	0.5046 (2.6945)	—0.8230 (—4.3943)	0.0786 (0.4195)
C^1C^1B	—0.8308 (— 3.9437)	0.2609 (1.2386)	—0.1115 (—0.5293)
P^3L	—0.6359 (— 8.1650)	—0.5378 (—6.9055)	—0.3778 (—4.8510)
P^3W	—0.1942 (— 2.5283)	0.5608 (7.3000)	0.3343 (4.3513)
M^1W	0.3598 (2.9161)	0.3197 (2.5909)	—0.0829 (—0.6716)
M^3L	0.5792 (11.6451)	0.4151 (8.3463)	0.3407 (6.8502)
M^3W	0.4296 (5.4312)	0.2967 (3.7512)	0.0365 (0.4615)
I_1M_3	0.0671 (0.2776)	0.0518 (0.2143)	0.7001 (2.8949)
DL	—1.0822 (— 3.4180)	—1.0652 (—3.3645)	—0.5902 (—1.8640)
Constant	42.2937	—14.8485	—17.1856
Variation explained (%)	72.1	17.4	10.6

(b)

Character	Function 1	Function 2	Function 3
TIL	0.8608 (0.6559)	0.3528 (0.2688)	—0.1414 (—0.1077)
TOL	0.3827 (1.0189)	—0.4860 (—1.2942)	0.4276 (1.1385)
FA	0.4753 (0.2519)	—0.1664 (—0.0882)	0.0245 (0.0130)
D3MC	—0.7691 (—0.5350)	—0.5986 (—0.4164)	—0.5699 (—0.3965)
D4MC	0.3866 (0.2713)	0.3145 (0.2207)	1.4964 (1.0500)
D4P1	—0.5181 (—0.7573)	0.5622 (0.8217)	0.2315 (0.3384)
D4P2	—0.2898 (—0.4659)	0.3955 (0.6357)	0.5888 (0.9465)
D5MC	—0.1078 (—0.0810)	0.7453 (0.5601)	—1.3136 (—0.9873)
D5P2	0.3186 (0.5073)	—0.4868 (—0.7751)	—0.2507 (—0.3991)
Constant	—9.5566	—16.0724	—3.34420
Variation explained (%)	66.4	22.4	11.2

The Western Group (all localities separate)

DFA based on skull characters of specimens from within the Western group (Madura, Java, Sumatra and associated small islands) revealed at least four distinct clusters (Figure 27a). These were (1) *Hipposideros m. madurae*; (2) *H. m. jenningsi*; (3) *H. sorenseni* and (4) *H. l. larvatus*. The last group shows further separation, particularly Candi (W. Java), Aceh and Palembang (Sumatra) and Nias I.

The Western Group (grouped by species and subspecies)

The DFA based on all 31 skull characters of the taxa: *H. l. larvatus, H. m. madurae, H. m. jenningsi* and *H. sorenseni* with the Sukabumi specimen unallocated, extracted three significant functions which combined account for 100% of the variation (function 1, 72.0%; function 2, 17.4% and function 3, 10.6%). All cases were correctly allocated to their designated taxon. The single Sukabumi specimen grouped closely with *H. larvatus.* The four taxonomic groups cluster approximately equidistantly in discriminant function space (Figure 28). *Hipposideros m. madurae* and *H. larvatus* separate from each other and from *H. m. jenningsi* and *H. sorenseni* on function 1. Characters loading heaviest on this function relate to overall size of skull (Table 4a) [greatest skull length (GSL), mastoid breadth (MB), rostrum length (RL), distance outside upper canines (C^1C^1B) and dentary length (DL)]; they are a reflection of the larger overall size of *H. larvatus. H. m. jenningsi* and *H. sorenseni* separated from *H. m. madurae* and *H. larvatus* and from each other on function 2. Characters loading heaviest on function 2 are dentary length, width of posterior palate (M^3M^3B), and cranial length (PIL) (Table 4a).

The DFA, based on a subset of 13 *external characters* listed in Table 1 (excluded were SVL, TVL, and EL which were missing from a number of specimens) of the four taxa in the Western group, with the Sukabumi specimen unallocated, also extracted three significant functions which combined explained 100% the variation (function 1, 66.4%; function 2, 22.3%; and function 3, 11.3%), but with only 74.1% of cases correctly allocated to their given taxonomic group. Three taxa: *H. m. madurae, H. m. jenningsi* and *H. sorenseni* formed reasonably discrete clusters from each other in discriminant function space (Figure 28b). The separation between *H. m. madurae* and both *H. m. jenningsi* and *H. sorenseni* was principally on function 2. Characters loading most heavily on function 2 were digit 3 metacarpal length (D3MC), digit 4 phalanx 1 length (D4P1) and digit 5 metacarpal length (D5MC) (Table 4b). *H. m. jenningsi* was separated from the other three taxa principally on function 1. Characters loading most heavily on this function were: tibia length, (TIL) digit 3 metacarpal length (D3MC), and digit 4 phalanx 1 length (D4P1) (Table 4b). The *H. larvatus* cluster overlaps extensively with *H. sorenseni* and less so with *H. m. madurae*.

The Sukabumi specimen clusters closest to *H. m. madura.*

The separation of the Western Group taxa (*H. m. madurae; H. m. jenningsi; H. sorenseni;* and *H. larvatus*) using DFA on 31 skull and 13 external characters (Figure 28) was also achieved from a considerably reduced character set, because of the extent of correlation between many of these characters. For example, similar clusters were obtained using only 10 skull characters (ZB, RH, NIW, NIL, P^3W, TBB, RL, P^3L, M^3W and

C^1C^1B) and 6 external characters (TIB, TOL, D4P1, D5MC, D2MC, D3MC). These characters were selected using a stepwise discriminant analysis; characters are listed in decreasing order of importance.

The Nusa Tenggara Group

The DFA based on 31 skull characters of specimens from within Nusa Tenggara, grouped by island, extracted five significant functions which explained 100% of the variance (function 1 — 55.4%, function 2 — 23.6%, function 3 — 8.2%, function 4 — 6.6% and function 5 — 6.2%). A plot of functions 1 and 2 and functions 2 and 3 (Figures 29a, b) shows that all island populations were distinct with the possible exception of the Semau population. 97.7% of all specimens were classified correctly into their island of capture. The two misclassification involved the Semau population; in one case a specimen from Semau was classified to the Roti population; in another a Sumbawa specimens was classified to the Semau population. If the above DFA was run without the four Semau specimens, 100% of the remaining island specimens (Sumbawa, Timor, Roti, Savu and Sumba) were correctly classified. Placing the Semau specimens as ungrouped in the above DFA allocated these specimens accordingly: two to Sumba, one to Roti and one to Sumbawa.

From Figures 29a,b the population on Sumbawa (Inner Banda Arc) was separated from populations on islands in the Outer Banda Arc (Roti, Savu, Semau, Timor and Sumba) principally on the important function 1 which explained 55.4% of the variance and from Savu on the less important function 3 (8.2% of the variance). The canonical discriminant function coefficients that loaded heavily on function 1 (in descending order of importance) are: least interorbital width (LIOW); M^2 length (M^2L); rostrum length (RL); M^1 width (M^1W) and on function 3 are: braincase width (BW); cochlea width (CW); rostrum length (RL); M^1 width (M^1W), PM^3 width (P^3W), and zygomatic breadth (ZB) (Table 5a). These characters related to shape of skull and cochlea and particularly molar teeth. Islands in the outer Banda Arc were separated on functions 2 and 3 (Figures 29a, b). In addition to function 3, discussed above, characters that loaded heavily on function 2 were: cochlea width (CW); M^3M^3 breadth (M^3M^3B); M^3 width (M^3W); palatal bridge length (PBL); braincase width (BW) and premaxilla length (PML). These added shape of palate to the above important discriminating characters.

The DFA based on all 16 external characters (present in all Nusa Tenggara specimens) grouped by island, extracted two significant functions which combined explained 88.3% of the variance (function 1, 74.5% and function 2, 13.8%). 84.5% of all cases were correctly classified to their island group. The plot of functions 1 and 2 (Figure 29c) indicated that *H. s. rotiensis* clustered separately from *H. sumbae* subsp. indet. A (Semau) and *H. sumbae* subsp. indet. B (Savu) on function 2. Characters loading heavily on this function were: forearm length (FA); digit 3 phalanges 1 and 2 lengths (D3P1, D3P2), digit 4 metacarpal length (D4MC) and digit 4 phalanx 1 length (D4P1) (Table 5b). *H. s. rotiensis*/ *H. sumbae* subsp. indet. A separated from *H. s. sumbae*/ *H. sumbae* subsp. indet. B/ *H. s. sumbae* on function 1. Characters loading heavily on function 1 were: ear length (EL) and digits 3 and 4 phalanx 1 length (D3P1, D4P1) (Table 5b).

Table 5 Canonical variate function coefficients for the significant functions for the Nusa Tenggara island groups (Sumbawa, Sumba, Savu, Roti, Semau, Timor). Standardised values followed by (in brackets) unstandardised values. (**a**) skull and (**b**) external characters.

(a)

Character	Function 1	Function 2	Function 3
GSL	0.3478 (1.0891)	—0.0398 (—0.1245)	0.2469 (0.7731)
BW	0.0396 (0.1952)	0.4178 (2.0581)	0.6373 (3.1393)
ZB	—0.0268 (—0.0989)	—0.3634 (—1.3431)	—0.4465 (—1.6503)
CH	0.1273 (0.8477)	—0.2439 (—1.6238)	0.3206 (2.1346)
RL	0.5171 (2.8372)	0.0367 (0.2016)	—0.5156 (—2.8290)
LIOW	—0.7702 (—4.7293)	0.2908 (1.7857)	—0.1985 (—1.2187)
PBL	0.2953 (1.7465)	—0.4217 (—2.4946)	—0.3446 (—2.0384)
PML	0.1913 (1.1122)	—0.4047 (—2.3524)	0.0280 (0.1626)
MF	0.3069 (2.2622)	—0.0095 (—0.0699)	0.2015 (1.4856)
TBL	0.1825 (1.4729)	—0.1246 (—1.0051)	—0.3405 (—2.7475)
TBB	0.1315 (0.6375)	0.3325 (1.6124)	0.0167 (0.0808)
NIW	0.3724 (2.8261)	—0.3356 (—2.5462)	0.0395 (0.3000)
CW	—0.3585 (—2.5482)	—0.6693 (—4.7566)	0.5911 (4.2012)
M^3M^3B	0.1182 (0.8104)	0.6037 (4.1372)	—0.1933 (—1.3247)
C^1C^1B	—0.0973 (—0.5407)	0.3091 (1.7173)	0.3238 (1.7991)
P^3W	—0.1106 (—1.5210)	0.0474 (0.6511)	—0.4557 (—6.2660)
M^1W	—0.4869 (—3.9613)	0.0931 (0.7571)	0.4590 (3.7338)
M^2L	0.5520 (6.8713)	—0.0771 (—0.9597)	—0.1037 (—1.2903)
M^2W	0.1197 (1.1381)	0.2534 (2.4083)	0.1220 (1.1593)
M^3W	—0.2211 (—2.7501)	0.4649 (5.7829)	0.1539 (1.9148)
Constant	—69.0830	—21.9855	—23.0779
Variation explained (%)	55.4	23.6	8.2

(b)

Character	Function 1	Function 2
SVL	—0.2459 (—0.1185)	0.1767 (0.0851)
TVL	0.0851 (0.0448)	0.7291 (0.3836)
EL	0.8480 (1.1264)	—0.0330 (—0.0438)
TIL	0.3890 (0.6274)	—0.0582 (—0.0939)
FA	—0.2768 (—0.2014)	—0.8281 (—0.6024)
D2MC	—0.4262 (—0.3683)	0.2956 (0.2554)
D3P1	0.6980 (1.0567)	—0.6689 (—1.0127)
D3P2	—0.2062 (—0.2135)	0.6213 (0.6433)
D4MC	—0.1708 (—0.1869)	0.7281 (0.7966)
D4P1	0.5756 (1.2071)	0.0860 (0.1805)
D4P2	—0.4318 (—0.8417)	—0.3498 (—0.6819)
Constant	—20.0799	—12.0670
Variation explained (%)	74.5	13.8

The separation of the Nusa Tenggara group taxa (*H. s. sumbae, H. s. rotiensis, H. s. sumbawae*) using DFA on 31 skull and 16 external characters (Figure 29) was also achieved from a considerably reduced character set because of the extent of correlation between many of these characters. For example, very similar clusters were obtained using only 6 skull characters (GSL, CW, M^3M^3B, BW, PML, RL) and 6 external characters (EL, D3P1, D4MC, SVL, TVL, FA). These reduced character sets were selected using a stepwise discriminant analysis; characters are listed in decreasing order of importance.

General Discussion

This study clarifies considerably the taxonomic status of the *Hipposideros* previously attributed to *H. larvatus sumbae* from Sumba and other islands in Nusa Tenggara. This was its major focus. However, examination of an extensive series of related specimens, also previously attributed to *H. larvatus*, from Java, Sumatra and associated islands — and a few specimens from Peninsular Malaysia (2), Sarawak (1) and Thailand (1) has only partially resolved their taxonomic status.

Specimens from Nusa Tenggara are *Hipposideros sumbae*. Most islands in Nusa Tenggara with *H. sumbae* have a morphologically distinctive form of the species. Populations on Sumba I., Roti I. and Sumbawa I. are considered separate subspecies, as probably also are those from Savu I. and Semau I. Only single specimens were available from Timor I. and Flores I. (the latter with a dentary damaged during its development by a disease and/or accident).

Specimens from Java, Sumatra, Madura, Nias, Krakatau and Palau Laut Is are very distinctive morphologically from *H. sumbae*. Three species (*H. madurae, H. sorenseni, H. larvatus*) and a possible fourth species from Sukabumi, are described from Java.

The nomenclature of this group of species is very difficult to resolve. This is because Horsfield (1823) recognised four species from Java. These are: *H. insignis, H. deformis, H. vulgaris* and *H. larvatus*. Their collection locality is known only as 'Java'. Their holotype or "co-types" lodged in the British Museum of Natural History are unavailable to us to study directly and have never been even remotely adequately described. All authors since Horsfield (1823, 1824) have considered the first three forms synonymous with *H. larvatus*. Temminck (1835) considered *H. vulgaris* to be a female of *H. insignis*. The cotype of *H. insignis* (BMNH 60.5.4.16 and 79.11.21.94) according to Tate (1941) have 'skulls' that consist of fragments of toothrows only (BMNH 60.5.4.16) or have the basal part of the cranium destroyed (BMNH 79.11.21.94). The type of *H. vulgaris* (BMNH 79.11.21.575) has the back of its braincase broken. Tate (1941) was apparently confused about the specimen BMNH 79.11.21.94. He referred to it as both a cotype of *H. insignis* and as the holotype of *H. deformis* (which he could not photograph). Ms Paula Jenkins, British Museum (Natural History), confirms that BMNH 79.11.21.94 is in fact the holotype of *H. deformis* and that it has the base of the cranium broken. Ms Jenkins also adds that "the skull of the types of *H. larvatus* BMNH 79.11.21.93 is inside the dried skin and the specimen is in such poor condition that I am unwilling to attempt to remove the skull and provoke even more disintegration". A decision with which we concur.

Table 6 Forearm lengths for *Hipposideros* spp. measured in this study.

Species	Locality	Forearm length x, range, sample size
H. l. larvatus	W. Java, Krakatau, Pulau Laut, Sumatra, Nias	57.5 (53.2-62.1) 60
H. l. larvatus	Sarawak	56.9, N = 1
H. l. larvatus	Pen. Malaysia	58.5 (57.8-59.2) 2
H. madurae	Madura I., Semarang, C. Java	55.0 (53.0-57.9) 15
H. sorenseni	Pangandaran, C/W Java	57.5 (55.4-60.2) 7
H. sumbae	Nusa Tenggara	54.0 (49.9-57.1) 86
H. sp. indet.	Sukabumi	57.6 (56.5-58.7) 2
H. sp. cf. *H. grandis*	Chanthaburi, SE Thailand	54.0, N = 1

It is not possible to know for certain where in Java Horsfield's type of *H. larvatus, H. insignis, H. deformis* and *H. vulgaris* were collected, but it is likely that the bulk of his collections came from W. Java, although he travelled widely over Java (Horsfield 1822-1824). The forearm length for types of *H. larvatus, H. deformis* and *H. vulgaris* listed by Tate (1941) as 53, 53 and 56 mm, respectively, also do not help in allocating our Javanese taxa to one of these named Javanese forms, although 53 mm is the lowest value reported by us for 60 specimens from W. Java. Measurements of forearm lengths for our Javanese forms overlap and are not diagnostic (Table 6). Further we are unsure as to whether or not all of Horsfield's types were adult. On the basis of measurements of these Javanese types provided to us by Ms Paula Jenkins (see Appendix), we are able to confidently state that none of the types *H. insignis, H. deformis* or *H. vulgaris* represent the taxon *H. madurae*. Further, the measurements of these types are similar to our W. Javan specimens considered by us to represent *H. l. larvatus*, rather than those from Pangandaran (*H. sorenseni*). For this reason we concur with most recent workers in considering *H. insignis, H. deformis* and *H. vulgaris* consubspecific with *H. l. larvatus*. However, confirmation of this will depend on a more detailed comparison of the skull of the *H. l. larvatus* holotype with these other forms, perhaps using x-ray techniques. However, without baculum and glans penis of these types (which are unavailable — they are dry skins and the *vulgaris* holotype is a female) to compare with W. Javan and Pangandaran specimens, it will be difficult to distinguish if the types represent members of the W. Javan or the Pangandaran taxa from the skull measurements that can be taken from these damaged types.

This study has shown that specimens from populations in W. Java, Sumatra, Pulau Laut I., Krakatau Is and Nias I. are similar in skull, external morphology, glans penis and baculum (specimens from Carita, Krakatau Is, Ujong Kulon, Aceh and Nias I. had a glans penis and baculum available for examination). Hill (1963) placed the Sumatra and Nias I. specimens in the subspecies *H. larvatus neglectus*. This subspecies was described from Borneo by Sody (1936) on the basis of specimens from C. Borneo having a forearm of 62-63. These values overlap with the *H. l. larvatus* in this study and are larger than the single specimen from Sarawak examined by us (Table 7). This Sarawak specimen and two from Pahang, Peninsular Malaysia, examined by us (forearms 57.8-59.2) also had glans penis and baculum of the same form as our *H. l. larvatus* specimens as did a specimen of *H. larvatus* illustrated in Zubaid and Davison (1987). Further, when these three Malaysian specimens are included in the DFA they cluster closely with the *H. l. larvatus* specimens. For these reasons we suspect that *H. l. larvatus* and *H. l. neglectus* are synonymous.

The single specimen from Chanthaburi, S.E. Thailand, examined by us is, however, morphologically quite distinct from *H. larvatus*, for example, its overall skull morphology (it clusters closer to *H. madurae* than it does to *H. l. larvatus*) and its glans penis and baculum morphology is distinct from all other taxa dealt with in this study. The baculum (Figure 5k) is almost identical to those figured as *H. l. larvatus* in Topál (1975: Plate 6, 5-10) from Tuong Linh, N. Vietnam. Clearly the Vietnam and Thailand specimens are not representative of *H. l. larvatus* as defined by us. Our Thailand specimen would also appear to be much smaller than the measurements of *H. grandis* presented from Chiangmai, N. Thailand, by Shamel (1942). For example (our measurements, followed by Shamel's in brackets) are total body length 57.2 (69-71); tail length 31.8 (34-35); forearm length 54.0 (62.0-66.2); skull condylobasal length 18.2 (?) (20.5-20.5); maxillary tooth row length 8.2 (8.6-8.8). However, on geography our Thailand specimen would appear to be a small representative of the form *grandis*. If this is the case, then the distinctive appearance of the baculum and skull of our specimen would suggest that *H. grandis* is a species.

This study confirms a number of previous studies by us that Nusa Tenggara is a unique biogeographic region which has been the centre of considerable speciation of mammals (Kitchener *et al.* 1992a). As indicated in our study of *Taphozous* (Kitchener *et al.* 1992b), the islands in the Outer Banda Arc (Sumba, Savu, Roti, Semau, Timor) showed considerable morphological, if not genetic, variation from the islands of the inner Banda Arc (Sumbawa and Flores). This again suggests that there is either very restricted gene flow between populations of *Hipposideros sumbae* in the inner and outer Banda arcs, or that *Hipposideros sumbae* in these different island arcs experience considerably different selection pressures and environments that influence their morphology.

Specimens Examined (see Figure 1 for map of localities)

Hipposideros larvatus larvatus

Pulau Panjang, Krakatau Is. (loc 1); 6♂♂, 11♀♀; MZB (9433, 14515 A-F), WAM (M25925-35). *Pulau Rakata* (Krakatau Is) (loc. 2); 3♂♂, 3♀♀; WAM (23305-11). *Ujong Kulon*, W. Java (loc. 3); 2♂♂; MZB 10607A-B. *Carita*, W. Java (loc. 4); 8♂♂, 5♀♀; MZB 1458A-C, WAM (M26420-25, M26427, M26429-

30, M26433). *Candi*, W. Java (loc. 5); 2♀♀; MZB (14853, 14887). *Banten*, W. Java (loc. 6); 2♀♀; MZB (14850, 10598). *Cikajang*, W. Java (loc. 7); 2♂♂; MZB 14860-61. *Rawa Kalong, Pelabuan Ratu*, W. Java (loc. 8); 1♂; MZB 10604. *Ciampea* W. Java (loc. 9); 1♂, 3♀♀ MZB 172A-B,D, MZB 9425. *Pulau Laut*, nr W. Java (loc. 11); 3♂♂, 1♀; MZB (9442-43, 10616A-B). *Aceh*, N. Sumatra (loc. 12); 2♂♂, 1♀; MZB (11279-80, 11283). *Palembang*, S. Sumatra (loc. 13); 1♂, 1♀; MZB (14854, 14886). *Nias I.*, nr N. Sumatra (loc. 14); 3♂; WAM (M37184, M37226, M37314).

Hipposideros larvatus subsp. cf *larvatus*
Pahang, Pen. Malaya (loc. 15); 1♂, 1♀; WAM 21156-57. *Bako National Park*, Sarawak (loc. 16); 1♂; WAM 23752.

Hipposideros madurae madurae
Holotype: *Sampang*, Madura I. (loc. 17); 1♂; MZB 10613B. Paratypes: *Sampang*, Madura I. 1♂, 3♀♀; and *Sumenep*, Madura I. (loc. 18); 2♂♂, 1♀; MZB 10615A-C.

Hipposideros madurae jenningsi
Holotype: *Semarang*, C. Java (loc. 19); 1♀; MZB 14883. Paratypes: *Semarang*, C. Java; 3♂♂, 3♀♀; MZB (14851, 14855-56, 14862, 14880, 14884).

Hipposideros sorenseni
Holotype: *Gua Kramat*, Pangandaran, C. Java (loc. 20); 1♀; MZB 11333. Paratype: *Gua Kramat*, Pangandaran; 2♂♂, 3♀♀; MZB (10612A-F).

Hipposideros sp. cf. *H. grandis*
Chanthaburi, Thamai, Khao wong kot, Thailand (loc. 21); 1♂, WAM M26828.

Hipposideros sumbae sumbae
Waikabubak, Sumba I. (loc. 22); 1♂, 3♀♀; WAM (M30315-17, 30319). Waikelasawah, Sumba I. (loc. 23); 1♂, 1♀; WAM (M30338, M30348). Waeelonda, Sumba I. (loc. 24); 1♂, 3♀♀; WAM (M30448, M30452-53, M30455). *Bondokodi*, Sumba I. (loc. 25); 1♂, 3♀♀; WAM (M30490-91, M30493, M30495).

Hipposideros sumbae rotiensis
Holotype: *Sangoen*, Roti I., Nusa Tenggara (loc. 26); 1♂; WAM M35436. Paratypes: 7 km SW *Baa*, Roti I. (loc. 27); 2♂♂, 1♀; WAM (M35361, M35369, M35379). *Sangoen*, Roti I.; 3♂♂, 3♀♀; WAM (M35433, M35435-36, M35438, M35440, M35442). Camplong, W. Timor (loc. 28); 1♂; MZB 14852.

Hipposideros sumbae sumbawae
Holotype: *Gua Batu Tering*, 3 km S Desa Batu Tering, W. Sumbawa I. (loc. 29). Paratypes: *Gua Batu Tering*, 3 km S Desa Batu Tering; 14♂♂, 16♀♀; WAM (M31140, M31515-16, M31416-17, M31439-40, M31462-63, M31468, M31492, M31495-99, M31515-16, M31528), MZB (11392, 11394-405). *Desa sangeang*, E. Sumbawa (loc. 30); 22♂♂, 1♀; WAM (M31526, M31529, M31532-34, M31536-37, M31539-40, M31542-43, M31545, M31549-52, M31553, M31559, M31564, M31566, M31568-69, M31571). *Gua Cermin*, nr Labuan Bajo, W. Flores (loc. 31): 1♂; MZB 14243.

Hipposideros sumbae subsp. indet. A.
Desa Uiasa, Semau I. (loc. 32); 1♀; WAM M35563. *Desa Onansila*, Semau I. (loc. 33); 2♂♂, 1♀; WAM (M38007-08, M38016-17).

Hipposideros sumbae subsp. indet. B.
Desa Menia, E. Savu I. (loc. 34); 2♂♂, 1♀, WAM (M35116, M35213, M35259, M35263).

Hipposideros sp. indet.
Gua Cidalog, Cikopeah, nr Sukabumi, W. Java (loc. 10); 1♂, 1♀; WAM M30008-09.

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Appendix

Measurements (in mm) of the skull of the holotypes of the Javanese names *Hipposideros insignis* (mandible only), *H. deformis* and *H. vulgaris* (both with basal part of cranium damaged).

Character	*H. insignis* BM 60.5.4.16	*H. deformis* BM 79.11.21.94	*H. vulgaris* BM 79.11.21.575
Palatal bridge length		4.46	3.91
M^3 width		2.63	1.92
P^3 width		1.80	1.72
Least interorbital width		3.31	3.03
C^1C^1 outer breadth		5.81	5.40
Dentary length		15.41	15.09
I_1M_3 length	10.66	10.56	10.03
Ramus to angular tip length		5.80	5.43
Nasal inflation length		6.08	6.10
Cranial length		*c.* 17.0	

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